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CONTENTS

M. G. Harasewych
Yuri I. Kantor
The deep-sea Buccinoidea (Gastropoda: Neogastropoda) of the Scotia Sea and adjacent abyssal plains and trenches 1

Lindsey T. Groves
New species of Late Cretaceous Cypraeidae (Gastropoda) from California and British Columbia and new records from the Pacific slope 43

Book Review 52

The deep-sea Buccinoidea (Gastropoda: Neogastropoda) of the Scotia Sea and adjacent abyssal plains and trenches

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ABSTRACT

Four new genera and species of buccinoidean gastropods, *Spikebuccinum stephaniae* new genus, new species; *Drepanodontus tatyanae* new genus, new species; *Muffinbuccinum catherinae* new genus, new species; and *Germonea rachelae* new genus, new species, are described from the Scotia tectonic plate and adjacent abyssal plains. Only *Bathydomus obtectus* Thiele, 1912, *Tromina bella abyssicola* Clarke, 1961 and *T. abyssorum* Lus, 1993, had previously been reported from abyssal depths off Antarctica. The latter two species were proposed in the genus *Tromina*, subsequently shown to belong to the family Muricidae. Therefore, a new genus, *Lusitromina* is proposed for these abyssal and hadal buccinoidean species. Analyses of the taxonomic placement, geographical and bathymetric distribution, and diversity of the 29 buccinoidean genera presently known from Antarctica and the Magellanic Province have shown that the abyssal (>2200 m) buccinoidean fauna of the region shares no genera with the sublittoral or bathyal faunas. None of the six abyssal genera conform readily to the subfamilies represented by the sublittoral or bathyal faunas. Credible sister taxa and likely origins for some abyssal genera occur on the adjacent continental slope. For others, closest relatives may be found on abyssal plains beyond the Antarctic convergence. Generic diversity decreases with increasing depth for both the bathyal and abyssal buccinoidean faunas, while bathymetric range tends to increase. For abyssal buccinoideans, maximum generic diversity occurs between 2600 and 3200 meters. The proportion of monotypic genera in the Antarctic and Magellanic Provinces is extraordinarily high (48.3%), and may be an artefact of low sampling density exacerbated by difficulties in differentiating closely related species. Neither gigantism nor dwarfism is evident in the abyssal buccinoidean fauna. Rather, the range in sizes narrows with increasing depth. Genera inhabiting the base of the continental slope are smaller than those of either the upper slope or continental rise. In the abyssal zone, maximum shell size is reached near the boundary of the continental rise and abyssal plain, and subsequently decreases with increasing depth.

INTRODUCTION

The Buccinoidea are the most geographically widespread and ecologically diverse clade within the Neogastropoda. First appearing during the Early Cretaceous [Valanginian] (Tracey et al., 1993), these predatory snails have radiated to occupy most benthic marine habitats ranging from the tropics to the poles and from the intertidal zone to hadal depths (Clarke, 1962). Several members of the families Nassariidae and Buccinidae have even invaded fresh water (Kantor and Kilburn, 2001; Brandt and Temcharoen, 1971).

Buccinoideans are readily distinguished by their usually weakly sculptured, conical to fusiform shells, their distinctive rachiglossan radula with multicuspid lateral teeth, long to very long proboscis, as well as by the absence of a rectal gland and accessory salivary glands. Their relationships to other Neogastropoda, however, have been variously interpreted, ranging from basal to derived (e.g., Ponder, 1974; Ponder and Warén, 1988; Ponder and Lindberg, 1996; Kantor, 1996; Harasewych et al., 1997). While a number of authors have attributed different taxonomic ranks to Buccinoidea and its component higher taxa (e.g., Powell, 1929; Thiele, 1929; Wenz, 1938; Ponder, 1974; Ponder and Warén, 1988), there is little disagreement as to the monophyly or composition of the group. We had earlier briefly reviewed the history of the higher classification of buccinoideans (Harasewych and Kantor, 1999), which is based primarily on differences in shell, opercular and radular morphologies applied to regional faunas (e.g., Powell, 1929, 1951, Southern Oceans; Habe and Sato, 1973, Northern Pacific; Bouchet and Warén, 1985, Northeastern Atlantic). We continue to retain provisionally the use of Buccinulidae and its subdivisions, as defined by Powell (1951), without necessarily endorsing their taxonomic rank, for the antiboreal members of the Buccinoidea, pending the availability of sufficient anatomical and/or molecular data for a meaningful phylogenetic revision of the higher taxa of Buccinoidea on a global basis. The subfamilial assignments of presently known buccinoidean genera that occur south of the Antarctic Convergence, as well as those from the Magellanic Province are reviewed (Appendix 1) and, in some cases, revised.

Our continuing studies of the Buccinoidea represented in the collections assembled by the United States Antarctic Program (USAP) have revealed a number of

previously undescribed taxa from the abyssal plains and trenches on and adjacent to the Scotia Plate. These taxa are described herein, and their affinities to other Antarctic and abyssal buccinoideans are discussed.

MATERIALS AND METHODS

This report is based primarily on buccinoideans sorted from the abyssal stations sampled by the United States Antarctic Program (USAP) vessels R/V Islas Orcadas and R/V Eltanin and housed in the collections of the National Museum of Natural History (USNM). Additional material, sampled by the German vessel R/V Polarstern and in the collection of the Zoological State Collection, Munich (ZSM) were made available through the kindness of Enrico Schwabe and Michael Schrödl.

In the material examined sections, "specimen" denotes that a preserved animal is present, while "shell" refers to a record based only on an empty shell. Anatomical descriptions are based on gross dissections of preserved specimens. Radulae were removed by gross dissection, cleaned using diluted bleach (NaOCl), coated with carbon and gold, and examined using a LEO 440 Scanning Electron Microscope. Photographs were taken using a Nikon D1 Digital Camera with a AF Micro Nikkor 60 mm lens. Images were processed using Adobe Photoshop 6.0.

The following abbreviations are used in the text: AL—aperture length, D—diameter, FWL—final whorl length, L—length, L/W—length/width, SCL—Siphonal canal length, SL—shell length, SW—shell width, W—width.

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Order Neogastropoda Wenz, 1938
Superfamily Buccinoidea Rafinesque, 1815
Family Buccinulidae Finlay, 1928
Subfamily Buccinulinae Finlay, 1928
Genus *Spikebuccinum* new genus

Type Species: *Spikebuccinum stephaniae* new species, by original designation.

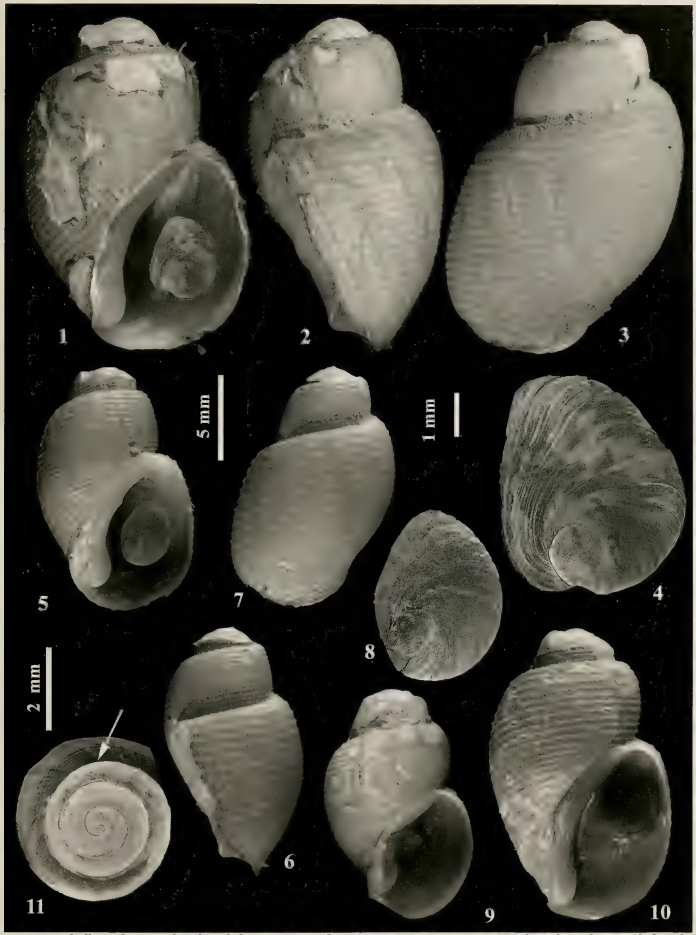
Description: Protoconch large (to 3.5 mm diameter), of 2⅔ smooth, evenly rounded, whorls. Teleoconch small (to 19.9 mm), very thin, translucent, ovate, rounded anteriorly, all but final 2–2½ whorls eroded. Shell sculpture of sharp, closely spaced, spiral cords. Columella weakly concave, shorter than aperture, producing siphonal notch with weak siphonal fasciole, short pseudoumbilicus. Periostracum finely hirsute. Operculum ovate, paucispiral, with subterminal nucleus, spans ~⅓ aperture length. Eyes absent. Buccal mass, odontophoral cartilages longer than retracted proboscis. Rachidian teeth tricuspid, with outer cusps broader, longer than central cusp. Lateral teeth with large outer, shorter inner cusp, with 3–4 denticles between. Salivary glands small, unfused. Gland of Leiblein glandular anteriorly, flaccid posteriorly. Posterior oesophagus forms crop before entering simple, U-shaped stomach, which has a well-defined gastric shield.

Etymology: This genus is named after Spike, a Cornish Rex cat that belongs to the senior author's daughter Stephanie.

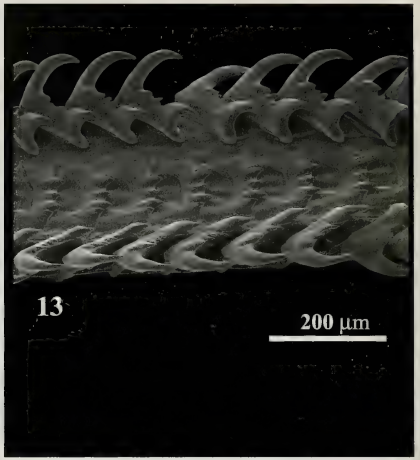
Spikebuccinum stephaniae new species
(Figures 1–23, Table 1)

Description: Shell (Figures 1–3, 5–7, 9, 10) small (to 19.9 mm), very thin, translucent, ovate, with rounded anterior, eroded spire. Protoconch (Figure 11), known from a single juvenile (Paratype 12), increasing in diameter from 0.4 mm to 3.5 mm, in 2⅔ smooth, evenly rounded, pitted whorls. Transition to teleoconch distinguished by slight change in color, from cream to white, and by abrupt transition from coarse, irregular axial growth striae, to finer, regular growth lines. Protoconch and upper whorls eroded on all other specimens. Extrapolation from growth series suggests that teleoconch may reach 5–6 whorls, of which all but last 2–2½ whorls eroded. Whorls evenly rounded, with indistinct shoulder, abutting suture. Axial sculpture limited to very fine, straight, strongly prosocline growth lines. Spiral sculpture of fine, sharp, uniform, evenly spaced cords (21–29 on final whorl, 11–14 on penultimate whorl). Aperture large (AL/SL = 0.60–0.67 when using length of eroded shell; AL/SL = 0.50–0.55, as estimated by linear projections of apex), broadly oval, deflected from shell axis by 22–25°. Outer lip very thin, not reflected, evenly rounded from suture to siphonal notch. Inner lip consists of a long, straight parietal region that meets the shorter, concavely indented axial portion of columella, ending in strong siphonal fold. Columella shorter than aperture, giving rise to a broad siphonal notch. Parietal callus uniformly narrow from suture to siphonal fold. Short, weak, siphonal fasciole and pseudoumbilicus present, often obscured by erosion. Shell color uniformly white. Periostracum very thin, straw yellow in color, with densely spaced axial lamellae, producing short, fine hairs at intersection with spiral cords, giving shell a finely hirsute appearance. Operculum (Figures 4, 8) small, spanning ~0.36 AL, yellowish brown, broadly ovate, paucispiral, with subterminal nucleus rotated relative to opercular axis.

Anatomy (Holotype): Soft tissues (Figures 14–22) comprise approximately 2¼ whorls. Mantle cavity spans just under ⅓ whorl, kidney ¼ whorl, digestive gland and gonad just under 1½ whorl. Columellar muscle short, broad, comprising slightly more than one whorl, attached to shell at rear of mantle cavity. Foot large, broadly rectangular (L/W ≈ 1). Body color yellowish tan, without pigmentation. Head large with long, thin tapering tentacles (Figure 15, tn), without neck. Eyes absent. Nephridium with semi-transparent walls that clearly reveal folds. Nephridial gland (Figure 14, ng) small, very narrow. Pericardium oriented antero-ventrally. Digestive



Figures 1–11. Shells and opercula of *Spikebuccinum stephaniae* new species. **1.** Apertural, **2.** lateral, **3.** and dorsal views of holotype, USNM 896368, off South Georgia Island, 53°02′ S, 37°40′00″ W, in 3056–3102 m [R/V Eltanin cruise 9, sta. 735]. **4.** Outer view of operculum of holotype. **5.** Apertural, **6.** lateral, and **7.** dorsal views of Paratype 1, USNM 1010626, from the type locality. **8.** Outer view of operculum of Paratype 1. **9.** Apertural view, USNM 1010630, E off South Sandwich Islands, 58°27′ S, 22°22′ W, in 4643–4645 m [R/V Eltanin sta. 603]. **10.** Apertural view, Paratype 8, USNM 1010629, S off Southern Georgia Island, 58°04′ S, 37°50′ W, in 3255–3166 m [R/V Eltanin sta. 699]. **11.** Scanning electron micrograph of protoconch of Paratype 12, ZSM (Zoological State Collection, Munich) 20021125, E off South Sandwich Islands, 58°24.98′ S, 25° 1.00′ W, in 2285.5 m, [R/V Polarstern cruise ANTXIX, sta. PS61/141-8, 22 Mar 2002] Arrow indicates transition to teleoconch. 5 mm scale bar applies to all shells, 1 mm scale bar applies to opercula, 2 mm scale bar applies to protoconch.



Figures 12–13. Radula of the holotype of *Spikebuccinum stephaniae* new species. **12.** Dorsal, and **13.** Left lateral (30°) views of the central portion of the radular ribbon.

gland lobes (Figure 19, adg, pdg) not fused, separated by ovary (Figure 19, ov).

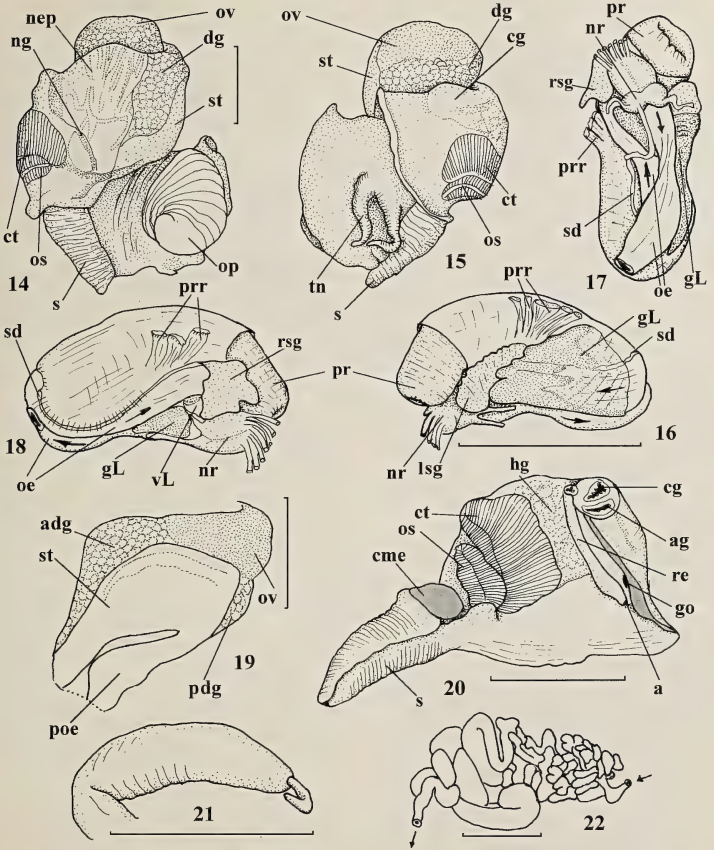
Mantle Cavity (Figure 20): Mantle cavity of medium width (L/W ~0.8), mantle edge slightly serrated. Siphon long (0.42 AL), free, muscular, extending substantially beyond mantle edge. Osphradium (Figure 20, os) small (~0.4 mantle cavity length) yellowish, bipectinate, with narrow osphradial nerve. Ctenidium (Figure 20, ct) large, very wide, spans about ¾ of mantle cavity length. The ctenidial lamellae are low. Hypobranchial gland lacks distinct folds, covered by thick layer of mucus.

Alimentary System (Figures 14–19): Proboscis (Figures 16–18, pr) of moderate length when retracted (~0.36 SL, 0.54 AL), thick (L/D ~3.3), smooth, nonpigmented. Proboscis retractor muscles (Figures 16–18, prr) not numerous, but thick, powerful, attached to proboscis sheath at mid-length when proboscis retracted. Proboscis sheath thin-walled, translucent along anterior half, thickened posteriorly, but thinner than proboscis wall. Proboscis wall thick, comprising ~1/10 of retracted proboscis diameter. Mouth opening dorso-ventrally compressed slit. Buccal mass muscular, large, filling retracted proboscis and protruding significantly beyond its rear. Odontophoral cartilages paired, fused anteriorly, slightly longer, than retracted proboscis. Radular ribbon longer than retracted proboscis, 5.4 mm long (0.41 AL), about 480 µm wide (0.037 AL), triserial (Figures 12–13), consisting of 58 rows of teeth, posteriormost 6 rows nascent. Rachidian teeth with 3 short cusps emanating from central portion of broad, anteriorly deeply arched basal plate. Central cusp slightly shorter, narrower than lateral cusps. Lateral teeth with long basal plate flanked by two main cusps, outermost nearly twice as long as innermost, 3–4 smaller, intermediate denticles vary in size and position from row to row, innermost denticle often abutting inner cusp.

Salivary glands (Figures 16–18, rsg, lsg) small, acinous, yellowish, not fused. Right salivary gland (rsg) dorsal to nerve ring, enveloping most of valve of Leiblein. Left salivary gland (lsg) lateral to, partially covering nerve ring. Salivary ducts (Figures 17–18, sd) thick, attached both to oesophagus and proboscis sheath by numerous connective tissue fibers. Salivary ducts pass along both sides of oesophagus, become "embedded" into oesophagus walls immediately after entering the proboscis. Valve of Leiblein (Figure 18, vL) well defined, large, pyriform, with whitish glandular pad containing ciliary cone visible through walls of valve.

Gland of Leiblein (Figures 16–18, gL) large, massive, glandular anteriorly; flaccid, transparent, lacking glandular tissue posteriorly; opens, via short duct, into oesophagus just posterior to nerve ring. Gland yellowish, only slightly darker than other organs of the cephalic haemocoel.

Oesophagus thick anterior to nerve ring, becoming thin-walled, flattened posterior to nerve ring. Oesopha-



Figures 14–22. Anatomy of *Spikebuccinum stephaniae* new species. **14–20.** Holotype. **21–22.** Paratype 1. **14.** Right, and **15.** Left lateral views of animal removed from shell. **16.** Left, **17.** ventral, and **18.** right lateral views of anterior alimentary system. **19.** Dorsal view of stomach, digestive glands and ovary. **20.** Mantle cavity organs. **21.** Lateral view of penis. **22.** Ventral view of seminal vesicle. Scale bars = 5 mm for **14–21,** 1 mm for **22. a,** anus; **adg,** anterior duct of the digestive gland; **ag,** albumen gland; **cg,** capsule gland; **cme,** cut mantle edge; **ct,** ctenidium; **dg,** digestive gland; **gL,** gland of Leiblein; **go,** female genital opening; **hg,** hypobranchial gland; **lsg,** left salivary gland; **nep,** nephridium; **ng,** nephridial gland; **nr,** circumoesophageal nerve ring; **oe,** oesophagus; **op,** operculum; **os,** osphradium; **ov,** ovary; pdg, posterior duct of the digestive gland; **poe,** posterior oesophagus; **pr,** proboscis; **prr,** proboscis retractors; **re,** rectum; **rsg,** right salivary gland; **s,** siphon; **sd,** salivary duct; **st,** stomach; **tn,** cephalic tentacles; **vL,** valve of Leiblein.

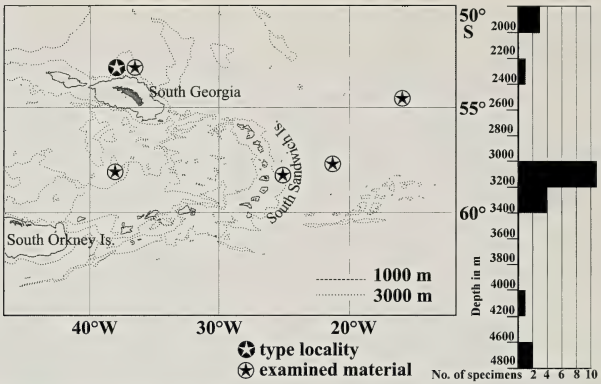


Figure 23. Geographic and bathymetric distribution of *Spikebuccinum stephaniae* new species.

gus widens to form a "crop" (Figure 19, poe) before entering stomach.

Stomach (Figures 14, 15, 19, st) relatively large, broadly U-shaped, without posterior mixing area. Due to poor preservation of holotype it was impossible to examine the internal morphology of the stomach in detail. Digestive gland ducts paired. Arrangement of stomach similar to *Lusitromina abyssorum* (Figure 132) but differs in having well developed, highly cuticularized gastric shield, with crescent-shaped dorsal side that is lifted and significantly protruded into stomach lumen.

Female Reproductive System: Female reproductive system typically buccinoidean, with small albumen gland partially overlapping posterior portion of capsule gland dorsally. Ingesting gland small, opening between albumen and long, broad capsule gland. Small bursa copulatrix situated anterior to capsule gland, tapering anteriorly to form female opening.

Male Reproductive System: Paratype 1, mature male. Seminal vesicle (Figure 22) of medium size, spans > ½ whorl, formed of numerous loops. Penis (Figure 21) long, narrow, non-pigmented, with slightly folded walls. Penial papilla long, cylindrical, surrounded by circular fold around base.

Type Locality: Off South Georgia Island, 53°02′ S, 37°40′ W, in 3056–3102 m [R/V Eltanin cruise 9, sta. 735, 13 Sep 1963].

Type Material: Holotype, ♀, USNM 896368; Paratypes 1–4, USNM 1010626, all from the type locality. Paratypes 5–7, USNM 1010628, off South Georgia Island, 53°26.7′ S, 36°32.6′ W, in 1967–2186 m, [R/V Islas Orcadas sta. 28, 12 May 1976]; Paratypes 8–11, USNM 1010629, S of Southern Georgia Island, 58°04′ S, 37°50′ W, in 3255–3166 m, [R/V Eltanin cruise 9, sta. 699, 30 Aug 1963]; Paratype 12, ZSM 20021125, E of South Sandwich Islands, 58°24.98′ S, 25° 1.00′ W, in 2285.5 m, [R/V Polarstern cruise ANTXIX, sta. PS61/141-8, 22 Mar 2002].

Table 1. *Spikebuccinum stephaniae* new species. Measurements of shell characters. Linear measurements in mm. (n = 7, including holotype. Juvenile specimens excluded).

Character	Mean	σ	Range	Holotype
Shell length (SL)	15.6	2.2	13.4–19.9	19.9
Final whorl length (FWL)	13.9	2.2	11.9–18.0	18.0
Aperture length (AL)	10.3	1.7	8.3–13.2	13.2
Shell width (SW)	10.1	1.6	8.6–13.2	13.2
FWL/SL	0.89	0.04	0.81–0.91	0.90
AL/SL	0.65	0.03	0.60–0.68	0.66
SW/SL	0.64	0.02	0.59–0.66	0.66
Number of spiral cords on penultimate whorl	12.4	1.0	11–14	14
Number of spiral cords on final whorl	24.6	2.9	21–29	29

Other Material Examined: USNM 896337, E of South Sandwich Islands, 54°51′ S, 14°54′ W, in 3947–4063 m, [R/V Eltanin sta. 1571, 28 Feb 1966], 1 specimen; USNM 1010630, E of South Sandwich Islands, 58°27′ S, 22°22′ W, in 4643–4645 m, [R/V Eltanin cruise 9, sta. 603, 5 May 1963], 1 specimen + 1 shell.

Distribution (Figure 23): The species is found in the Scotia Sea and adjacent abyssal plains at depths of 1967–4645 m.

Etymology: This species is named for the senior author's elder daughter, Stephanie Alexandra Harasewych.

Remarks: The shell morphology of *Spikebuccinum stephaniae* superficially resembles that of several species of *Chlanidota*, especially *C. signeyana* Powell, 1971 and *C.* (*Pfefferia*) *invenusta* Harasewych and Kantor, 1999, and, to a lesser extent, an eroded *Neobuccinum eatoni* (Smith, 1875). However, it can readily be distinguished from these taxa by its very short columella, an inconspicuous siphonal fasciole, as well as by having a rachidian tooth in which the central cusp is shorter and narrower, rather than longer and stouter than the outer cusps. The lateral teeth of all species of *Chlanidota* and the monotypic *Neobuccinum* have a strong, single intermediate cusp, rather than the multiple denticles of *Spikebuccinum*. The shell of *Spikebuccinum stephaniae* is also somewhat similar to that of *Antarctodomus okutanii* Numanami, 1996, which has a clearly cominelline radula, with tricuspid rachidian and bicuspid lateral teeth.

The radular morphology of *Spikebuccinum stephaniae* is distinctive, and suffices to distinguish it from all Antarctic and Magellanic buccinoideans. The presence of multiple denticles between the flanking cusps of the lateral teeth would appear to preclude the inclusion of this genus in the subfamily Buccinulinae, which is defined on the basis of having tricuspid rachidian and lateral teeth (Powell, 1951). However, Powell (1951:131) expanded this criterion to include *Bathydomus* Thiele, 1912, within Buccinulinae, citing the conchological affinities of *Bathydomus* to *Chlanidota*. We questionably include *Spikebuccinum* within the subfamily Buccinulinae, noting the possibly pleisiomorphic similarity of its radula to such boreal and temperate taxa as *Neptunea*, some *Buccinum, Cantharus* and certain *Busycotypus*.

The strongly paucispiral operculum of *Spikebuccinum stephaniae* is a feature it shares with a number of genera, among them *Neobuccinum, Parficulina* Powell, 1958, *Falsitromina* Dell, 1990, *Parabuccinum* Harasewych, Kantor and Linse, 2000, and such boreal genera as *Mohnia* Friele *in* Kobelt, 1878, and *Pararetifusus* Kosuge, 1976. While operculum morphology is undoubtedly useful for distinguishing genera, its utility for discerning phylogenetic relationships among supraspecific taxa is less clear.

Comparative anatomical data is available for only a very few buccinulid taxa, among them *Chlanidota* (Harasewych and Kantor, 1999) and *Parabuccinum* (Harasewych, Kantor and Linse, 2000). Of these, *Spikebuccinum* appears most similar anatomically to *Chlanidota*, but differs in having proportionally longer odontophoral cartilages, salivary glands that are not fused, a valve of Leiblein with a ciliary cone, a gland of Leiblein that opens to the mid-oesophagus via a narrow rather than broad duct, a broader stomach with a well-defined gastric shield, and a tapering rather than hemispherical bursa copulatrix.

Drepanodontus new genus

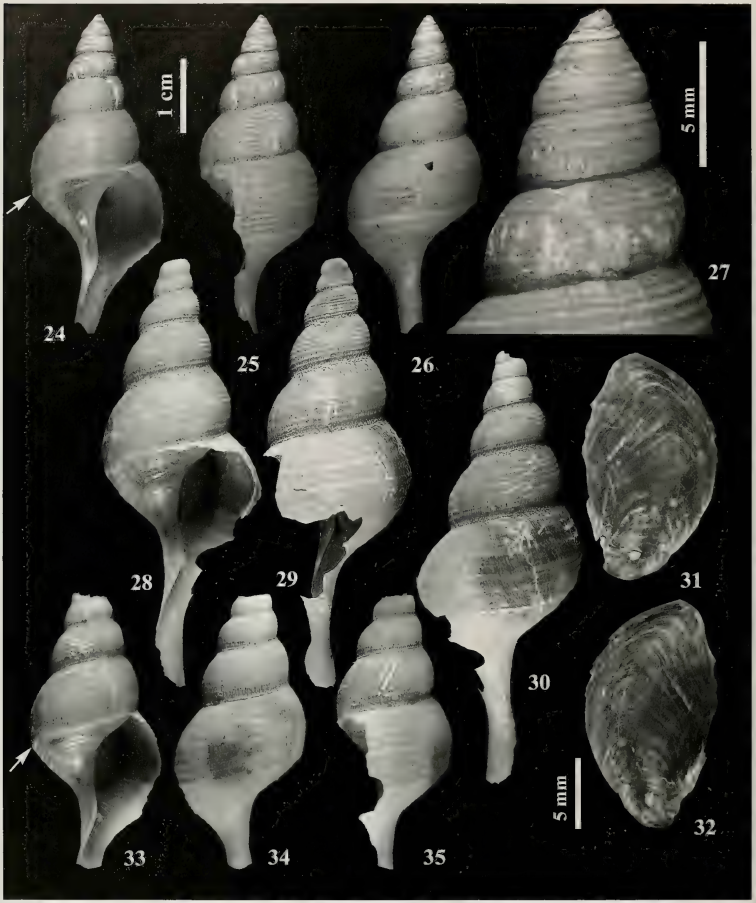
Type Species: *Drepanodontus tatyanae* new species, by original designation.

Description: Protoconch eroded. Shell large (to 56 mm), thin, strongly fusiform, with long, broad, open siphonal canal. Early whorls straight to concave, subsequently becoming convex. Whorls lacking shoulder, final whorl evenly convex from suture to distinct peripheral cord, evenly concave from peripheral cord to tip of siphonal canal. Sculpture of axial growth lines, most pronounced on early whorls, and strong, evenly spaced spiral cords. Aperture large, narrow, elliptical. Outer lip not reflected. Parietal region broad posteriorly, columella shorter than siphonal fold. Periostracum lamellose. Operculum large (~0.82 AL), oval, thin, translucent, with terminal nucleus. Head medium-sized, with short, stout tentacles, large eyes. Kidney large. Buccal mass small, odontophoral cartilages short. Rachidian teeth variable, tricuspid, cusps may be fused to appear monocuspid, or supplemental denticles or cusps may be present in some specimens. Lateral teeth with single, large, sickle-shaped cusp that may have one or more denticles. Salivary glands not fused, right gland much larger than left. Gland of Leiblein long, glandular anteriorly, tapering, flaccid posteriorly. Oesophagus broadens to form crop, constricts before entering very large, U-shaped stomach that lacks posterior mixing area.

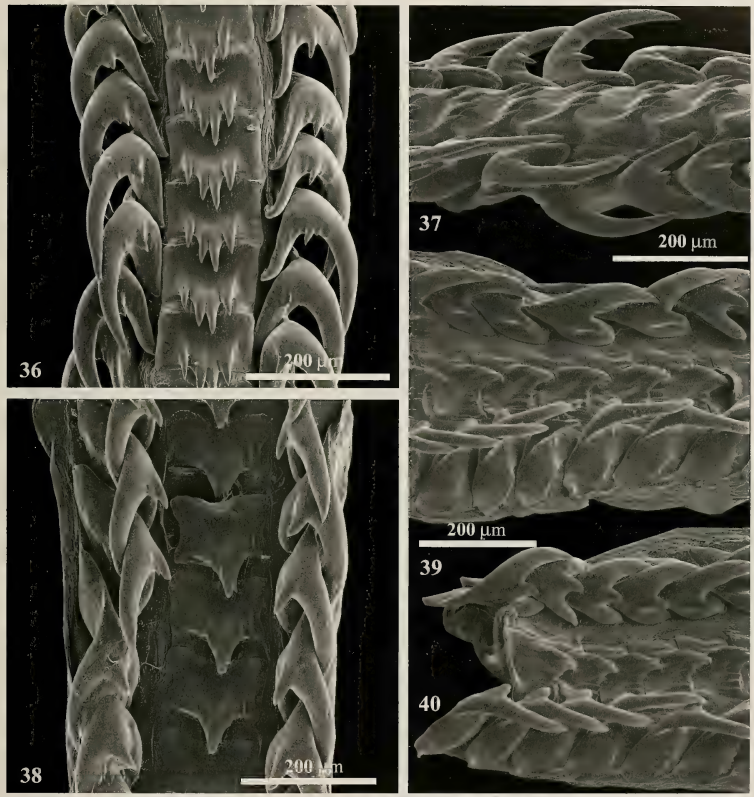
Etymology: *Drepane* (Gr.)—sickle, *odontos* (Gr.)—tooth. The name reflects the very unusual sickle shape of the lateral teeth, consisting of a long, narrow basal plate with a single, long, recurved outer cusp, often with one or more denticles along its inner edge.

Drepanodontus tatyanae new species
(Figures 24–50, Table 2)

Description: Shell (Figures 24–30, 33–35) large (to 43.1 mm), thin, strongly fusiform. Protoconch eroded on all specimens. Early whorls of holotype (Figure 27) indicate that protoconch would likely have been ~2–2½ whorls, < 3 mm in diameter. Transition to teleoconch indistinct in holotype. Teleoconch estimated to consist of up to 7 whorls. Early teleoconch whorls slightly concave in profile, with narrow spiral cords. By third whorl, teleoconch becomes convex, increasingly so in subsequent whorls, forming evenly rounded, oval whorls without distinct shoulder. Suture abutting onto pronounced peripheral cord (Figures 24, 33, arrow). Axial sculpture

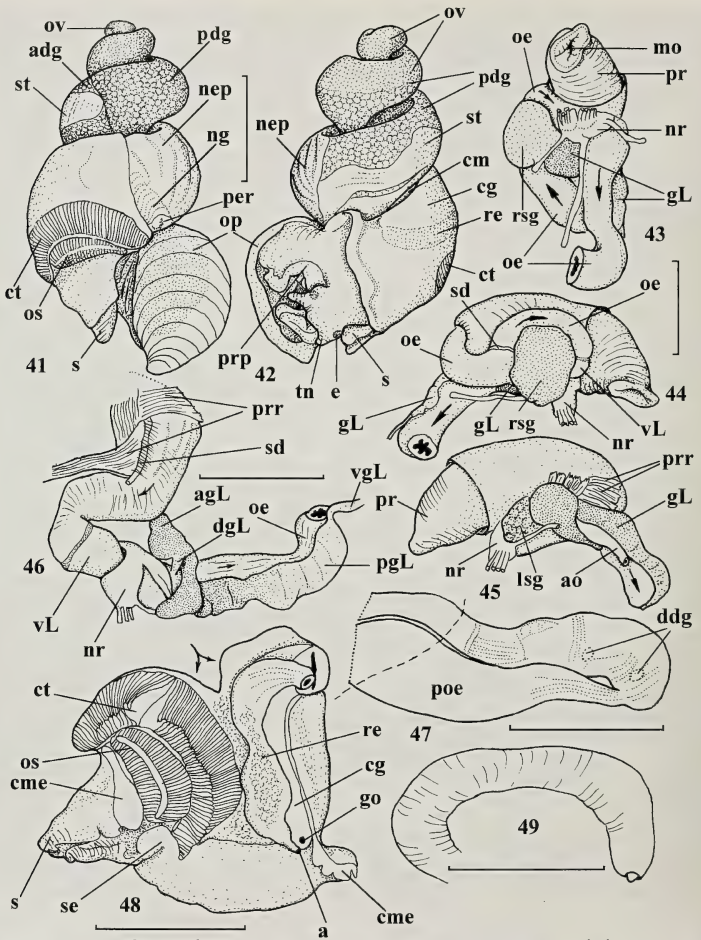


Figures 24–35. Shells and opercula of *Drepanodontus tatyanae* new species. **24.** Apertural, **25.** lateral, and **26.** dorsal views of the holotype, USNM 1010544, NE of South Shetland Islands, 59°01′ S, 52°00′ W, in 3010–3510 m. [R/V Eltanin cruise 22, Sta. 1511]. **27.** Enlarged upper shell whorls of holotype. **28.** Apertural, **29.** lateral, and **30.** dorsal views of Paratype 1, USNM 881529, E of South Sandwich Islands, 57°00.24′ S, 26°10.06′ W, in 2740–2757 m. [R/V Eltanin cruise 575, sta. 38]. **31.** Outer, and **32.** inner views of the operculum of Paratype 1. **33.** Apertural, **34.** lateral, and **35.** dorsal views of the shell of paratype 2, USNM 881529. Same locality as Paratype 1.



Figures 36–40. Radulae of *Drepanodontus tatyanae* new species. **36.** Dorsal, and **37.** left lateral (45°) views of the central portion of the radular ribbon of Paratype 1, USNM 881529. **38.** Dorsal, **39.** left lateral (45°) views of the central portion of the radular ribbon, and **40.** left lateral (45°) view of the bending plane of a non-type specimen, USNM 1010545, Argentinean Basin, 47°17.3′ S, 47°45.7′ W, in 5685–5798 m [R/V Islas Orcada, cruise 575, sta. 4].

of pronounced growth lines, opisthocyrt on early whorls, becoming weaker, orthocline by fourth teleoconch whorl. Spiral sculpture of broad, sharp cords (9–12 on penultimate whorl, 10–14 from suture to peripheral cord, 16–24 from peripheral cord to tip of siphon) narrower than intervening spaces, with 0–4 very fine threads between adjacent cords, especially near periphery. Peripheral cord, slightly thicker more pronounced that others, demarcates inflection in curvature of outer lip, evenly convex abapically, evenly concave from peripheral cord to tip of siphonal canal. Aperture large (AL/SL = 0.56), roughly elliptical, deflected from shell axis by 13–17°. Siphonal canal long (~¼ shell length), broad, open, crosses shell axis. Outer lip thin, not reflected. Inner lip of weakly concave parietal region, slightly longer columella, long siphonal fold extending



Figures 41–49. Anatomy of *Drepanodontus tatyanae* new species. (**41–48.** Paratype 1. **49.** Paratype 2, both USNM 881529). **41–42.** Lateral views of animal removed from shell. **43.** Ventral, **44.** right lateral, and **45.** left lateral views of the anterior alimentary system. **46.** Latero-dorsal view of the anterior oesophagus, showing the duct of gland of Leiblein. Oesophagus twisted counterclockwise. **47.** Dorsal view of stomach, dashed line indicates the posterior nephridial border. **48.** Mantle complex of organs. **49.** Lateral view of penis. Scale bars = 1 cm for Figures 41–42, 47–49, 5 mm for Figures 43–46. **a,** anus; **adg,** anterior duct of the digestive gland; **agd,** anterior lobe of digestive gland; **ao,** aorta; **cg,** capsule gland; **cm,** columellar muscle; **cme,** cut mantle edge; **ct,** ctenidium; **dgL,** duct of gland of Leiblein; **e,** eye; **gL,** gland of Leiblein; **go,** female genital opening; **lsg,** left salivary gland; **mo,** mouth opening; **nep,** nephridium; **ng,** nephridial gland; **nr,** circumoesophageal nerve ring; **oe,** oesophagus; **op,** operculum; **os,** osphradium; **ov,** ovary; **pdg,** posterior lobe of digestive gland; **per,** pericardium; **poe,** posterior oesophagus; **pr,** proboscis; **prp,** propodium; **prr,** proboscis retractors; **re,** rectum; **rsg,** right salivary gland; **s,** siphon; sd, salivary duct; **st,** stomach; **vL,** valve of Leiblein.

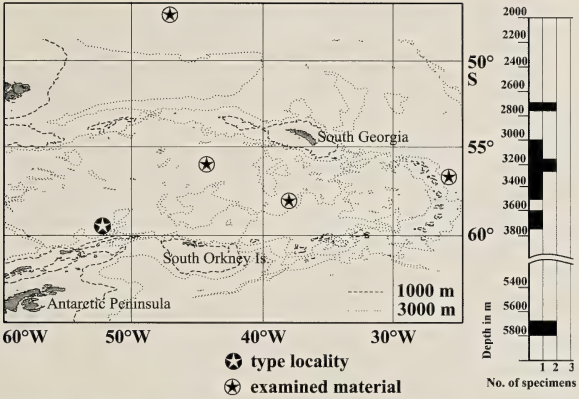


Figure 50. Geographic and bathymetric distribution of *Drepanodontus tatyanae* new species.

beyond glossy, translucent parietal region, broad posteriorly, tapering toward base of siphonal canal. Neither siphonal fasciole nor pseudoumbilicus present. Shell uniformly white, aperture, parietal callus glossy. Periostracum straw-colored, of widely spaced, short axial lamellae. Operculum (Figures 31–32, 41–42, op), large (~0.82 AL), oval, thin, brownish yellow, flexible, with terminal nucleus. Attachment of columellar muscle clearly visible through operculum, oval, spans about ⅔ of operculum surface.

Anatomy (Paratype 1): Soft tissues (Figures 41–42) comprise approximately 3½ whorls. Mantle cavity spans slightly less than ½ whorl. Kidney (Figures 41, 42, nep) broad, spans slightly less than ½ whorl, with 12 transverse folds of unequal width visible through wall. Nephridial gland (Figure 41, ng) narrow, situated anterodorsally to the nephridium. Digestive glands (Figures 41, 42, adg, pdg) of 2½ whorls. Columellar muscle (Figure 42, cm) of 1½ whorls, attached to shell at rear of mantle cavity. Foot medium-sized, short in contracted specimen (L/W ~1.2), with well-developed narrow propodium (Figure 42, prp) separated by narrow propodial cleft. Body color yellowish tan, without pigmentation. Head medium-sized, with short, stout, conical tentacles, with small but distinct lobes at their bases. Eyes present (Figure 42, e), light gray in color and semitransparent, deeply embedded into lobes. Mantle does not cover base of head.

Mantle Cavity (Figure 48): Mantle cavity deep (L/W ~1.2). Mantle edge smooth, slightly thickened. Si-

Table 2. *Drepanodontus tatyanae* new species. Measurements of shell characters. Linear measurements in mm. (n = 3, including holotype).

Character	Mean	σ	Range	Holotype
Shell length (SL)	45.1	10.1	36.2–56.0	43.1
Final whorl length (FWL)	33.8	7.4	28.6–42.2	30.5
Aperture length (AL)	26.7	6.2	22.2–33.7	24.1
Siphonal canal length (SCL)	11.4	4.7	7.5–16.7	10.1
Shell width (SW)	19.1	2.3	17.5–21.8	18.1
FWL/SL	0.75	0.04	0.71–0.79	0.71
AL/SL	0.59	0.03	0.56–0.61	0.56
SCL/SL	0.25	0.05	0.21–0.30	0.23
SW/SL	0.43	0.05	0.39–0.48	0.42
Number of spiral cords on penultimate whorl	10.0	1.5	9–12	10
Number of spiral cords suture to peripheral cord	12.0	2.0	10–14	12
Number of spiral cords peripheral cord to siphon	19.7	4.0	16–24	19

phon (Figure 48, s) short, free, muscular, broad, extending well beyond mantle edge, with thick siphonal edge (Figure 48, se), covering anteriormost part of ctenidium. Osphradium (Figure 48, os) greenish, bipectinate, large, wide, ½ as long, ⅔ as wide as ctenidium. Ctenidium (Figure 48, ct) large, curved, spanning nearly entire mantle cavity length. Ctenidial lamellae broad, triangular, with short recurved edges along posterior part (closer to pericardium), gradually becoming narrower, relatively taller anteriorly. Hypobranchial gland lacks distinct folds, covered by thick layer of mucus. Rectum long, spanning ~4/5 of mantle cavity length.

Alimentary System (Figures 41–47): Proboscis nonpigmented, (Figures 43, 45, pr) short when retracted (~0.2 SL, 0.58 AL), thick (L/D ~3), with slightly folded walls. Proboscis retractor muscles (Figures 45, 46, prr) not numerous, thin, attached to thin-walled, translucent proboscis sheath at middle-posterior region when proboscis retracted. Proboscis wall thin, ~1/10 proboscis diameter. Anterior part of proboscis flattened to form rim surrounding mouth opening (Figure 43, mo) in form of irregular triangular slit. Anterior oesophagus very broad, nearly filling proboscis. Dorsal folds very large, bordering deep groove. Buccal mass small, spans slightly more than ½ of proboscis length. Odontophoral cartilages paired, fused anteriorly, extend nearly entire length of buccal mass, but <½ proboscis length. Radular ribbon (Figures 36–40) equal in length to cartilages, 6.6 mm (0.35 AL), about 380 μm wide (0.020 AL), triserial, consisting of 50 rows of teeth, posteriormost 5 rows nascent. Rachidian teeth of Paratype 1 (Figures 36–37) with 4 cusps, here interpreted as comprising a long central cusp, flanked by shorter, outer cusps, with an additional, asymmetrical cusp on the left side. Rachidian teeth of a second specimen (Figures 38–40) appear monocuspid, but "central cusp" consists of 3 incompletely fused cusps, flanked by additional small denticles (Figure 40). Lateral teeth with distinctive shape, with single large, recurved outer cusp emanating from long, narrow basal plate. Inner surface of cusp with 1 or more, occasionally bifid, posteriorly directed denticles, with number, size of denticles varying from side to side and along radular ribbon.

Right salivary gland medium-sized, rounded, partially covering valve of Leiblein (Figures 43, 44, rsg), laterodorsal to nerve ring. Left salivary gland slightly smaller than right, irregularly shaped, dorsal to nerve ring, ventral to proboscis with its main axis perpendicular to proboscis axis, appears small when viewed from left (Figure 45, lsg). Salivary ducts (Figures 44, 46, sd) short, thick, enter oesophagus wall shortly after leaving gland. Valve of Leiblein (Figure 46, vL) well defined, large, pyriform, with whitish glandular pad visible through walls of valve.

Gland of Leiblein (Figures 43–45, gL) yellowish, slightly darker than other organs of cephalic haemocoel, medium sized, long, tubular, coiled anteriorly. Gland thin-walled, ascinous anteriorly (Figure 46, agL), opens into oesophagus slightly posterior to nerve ring via broad, short duct (Figure 46, dgL), becomes thinner, more transparent posteriorly (Figure 46, pgL), tapering to become flaccid, non-glandular (Figure 46, vgL).

Oesophagus thick, broad anterior to nerve ring, narrowing slightly posterior to the ring. Posterior oesophagus expands greatly to form "crop," (Figure 47, poe) then gradually narrows towards opening into stomach. Stomach (Figure 47) very large, spans ~½ whorl, from the posterior border of nephridium, U-shaped, without posterior mixing area. Preservation inadequate to discern internal morphology. Digestive glands ducts (Figure 47, ddg) large, paired, closely spaced. Posterior duct close to oesophagus entrance, anterior duct at midlength of stomach. Digestive glands clearly separate. Anterior gland small (Figure 41, adg), spans ~½ whorl, posterior gland ~2 whorls (Figures 41, 42, pdg). Glands meet at the level of the posterior duct to digestive gland. Rectum long, spans ~4/5 of mantle cavity length. Rectum thin-walled, very broad, filled with polychaete spicules, numerous sand grains of different sizes.

Female Reproductive System: Paratype 1, mature female. Pallial gonoduct consists of long, tubular, capsule gland (Figures 42, 48, cg), with a small bursa copulatrix anterior to it. Genital opening (Figure 48, go) below, slightly posterior to anus (Figure 48, a).

Male Reproductive System: Paratype 2, male. Penis (Figure 49) long, very narrow, flattened laterally. Seminal papilla very small, blunt, surrounded by deep circular fold around its base.

Type Locality: NE of South Shetland Islands, 59°01′ S, 52°00′ W, in 3010–3510 m. [R/V Eltanin cruise 22, Sta. 1511, 26 Jan 1966].

Type Material: Holotype, USNM 1010544, from the type locality. Paratype 1 ♀, Paratype 2 ♂, USNM 881529, E of South Sandwich Islands, 57°00.24′ S, 26°10.06′ W, in 2740–2757 m. [R/V Eltanin cruise 575, Sta. 38, 22 May 1975].

Other Material Examined: USNM 1010545, South Atlantic Ocean [Argentine Abyssal Plain], 47°17.3′ S, 47°45.7′ W, in 5685–5798 m. [R/V Islas Orcadas Cruise 575, Sta. 4, 8 May 1975], 2 bodies without shells (radula illustrated, Figures 38–40); USNM 1010546, Scotia Sea, S of South Georgia Island, 58°04′ S, 37°50′ W, 3255–3166 m. [R/V Eltanin cruise 9, sta. 699, 30 Aug 1963], 1 dead poorly preserved juvenile. USNM 1013084, Scotia Sea, SW of South Georgia Island, 55°56′ S, 44°56′ W, 3742–3614 m. [R/V Eltanin cruise 575, Sta. 472, 13 Feb 1963], 1 body and fragments of the shell.

Distribution (Figure 50): This species occurs in the Scotia Sea and adjacent Argentine Abyssal Plain, at depths of 2740–5798 m.

Etymology: This species is named in honor of the junior author's wife, Tatyana Steiker, an ichthyologist and illustrator at the P. P. Shirsov Institute of Oceanology.

Remarks: The large, elongate, fusiform, siphonate,

spirally corded shell of *Drepanodontus tatyanae* easily distinguishes this species from most Antarctic buccinoideans. Conchological similarity is limited to relatively few large taxa, notably *Antarctoneptunea aurora* (Hedley, 1912) and *Cavineptunea monstrosa* Powell, 1951, both members of continental shelf and upper slope faunas. *Drepanodontus tatyanae* is most easily distinguished from the former by having a distinctive peripheral spiral cord that demarcates a change in the direction of curvature in the outer lip, while the monotypic *Cavineptunea* is most easily distinguished by its unique, cylindrical, flat-sided, indented protoconch. Both *Antarctoneptunea* (Dell, 1972: fig. 6) and *Cavineptunea* (Powell, 1951: 145) have radulae with tricuspid rachidian teeth and lateral teeth with 3 (or 4) cusps, quite unlike the distinctive radula of *Drepanodontus*.

The radula of *Drepanodontus tatyanae* most closely resembles that of *Kapala bathybius* Bouchet and Warén, 1986 (Bouchet and Warén, 1986: fig. 8), a species inhabiting the Cape Basin off southwestern Africa at depths of 3550 m. Like *Drepanodontus*, *K. bathybius* has rachidian teeth that may appear to be monocuspid in some individuals, with anteriorly indented, squarish basal plates, and lateral teeth characterized by a single, large, sickle-like cusp with secondary denticles that vary in number and prominence from side to side and from tooth to tooth. The shell of *K. bathybius*, and the related *K. bonaespei* (Barnard, 1963), also from the Cape Basin in 2504–3103 m, are comparable in size, and also elongate, fusiform and spirally corded, but broader (Bouchet and Warén, 1986: figs. 42, 43), and lack the distinctive peripheral cord of *Drepanodontus*. Barnard (1963: 432, fig. 6b) illustrates and describes the radula of *K. bonaespei* (which he described as a *Neptunea*) to have rectangular rachidian teeth with a "median cusp, sometimes a minute denticle on one side or on both sides" and lateral teeth "unequally bicuspid, with 2–5 tiny denticles between the two cusps, the denticles not always symmetrical."

Barnard (1963) assigned this species to the genus *Neptunea* Röding, 1798, because of the similarity of its lateral teeth with those of boreal buccinoideans, despite striking differences in the morphology of the shell and rachidian teeth. Bouchet and Warén, (1986: 464) also commented on lateral tooth similarities of *Kapala* (including its type species, the southern Australian bathyal species *K. kengrahami* Ponder, 1982) with the type species of the boreal genera *Volutopsius* Mörch, 1857, *Neoberingius* Habe and Ito, 1965, *Ancistrolepis* Dall, 1895, and certain representatives of *Japelion* Dall, 1918. These boreal taxa have elongated, spatulate lateral teeth with a large outer cusp, a significantly smaller inner cusp, and a variable number of smaller denticles or cusps between them. We interpret the lateral teeth of *Drepanodontus* to be different, in that they have a single, large outer cusp, but lack the shorter inner cusp of the boreal taxa. While some of the denticles that frequently emerge from the inner edge of the cusp of *Drepanodontus* may be large enough to be confused with an inner cusp, the lateral teeth of the boreal species are fundamentally bicuspid, while those of *Drepanodontus* are fundamentally monocuspid. Interestingly, the radula of *K. bathybius* illustrated by Bouchet and Warén (1986: fig. 8) has monocuspid lateral teeth lacking denticles distally, but developing denticles proximally along the left side of the radula, while the lateral teeth on the right side have 1 large and 1–3 smaller denticles along the inner edge of the single cusp.

The operculum of *Drepanodontus* is large, ovate, and has a terminal nucleus. While all species of *Kapala* share this opercular morphology, it is not distinctive, but widespread throughout Buccinoidea.

Although the presence of large eyes is not surprising in the bathyal type species of *Kapala* (Ponder, 1982: fig. 2), their occurrence in the abyssal taxa *K. bonaespei* (Barnard, 1963: 432) and *Drepanodontus tatyanae* is noteworthy. Other anatomical features that are congruent between *Drepanodontus tatyanae* and *Kapala kengrahami* include a small buccal mass and odontophore, a large kidney, a large, well-developed valve of Leiblein, crop, and a simple stomach.

Drepanodontus tatyanae co-occurs with *Muffinbuccinum catherinae* at the type locality of that species.

Subfamily Prosiphiinae Powell, 1951
Muffinbuccinum new genus

Type Species: *Muffinbuccinum catherinae* new species, by original designation.

Description: Protoconch, early whorls eroded. Teleoconch of moderate size (to ~30 mm) very thin, chalky, with evenly rounded whorls, tapering anterior, short, broad siphonal canal. Sculpture of sharp, narrow axial ribs, crossing uniform, closely spaced spiral cords, occasionally forming finely reticulate surface sculpture. Aperture large, elongate, elliptical. Parietal region broader posteriorly. Columella short, not axial. Periostracum of very fine axial lamellae, not hirsute. Operculum, large (~0.56 aperture length), elongated, claw-like, with terminal nucleus and growth lines nearly perpendicular to long axis. Head large, with tapering tentacles lacking eyes. Columellar muscle short. Nephridium very narrow. Rachidian teeth broadly rectangular, with 3 cusps concentrated near center of tooth, central cusp longest. Lateral teeth as broad as rachidian tooth, roughly rectangular in outline, with 7–8 cusps of nearly equal length, outermost cusp, slightly shorter, stouter, weakly to strongly serrated along outer margin. Salivary glands large, fused ventrally. Gland of Leiblein long, narrowly tubular, highly coiled. Oesophagus muscular, does not widen before opening into stomach. Stomach very small, broadly U-shaped, lacks posterior mixing area. Rectum short, narrow, with terminal papilla.

Etymology: This genus is named after Muffin, a domestic shorthair cat that belongs to the senior author's daughter Catherine.

Muffinbuccinum catherinae new species
(Figures 51–76, Table 3)

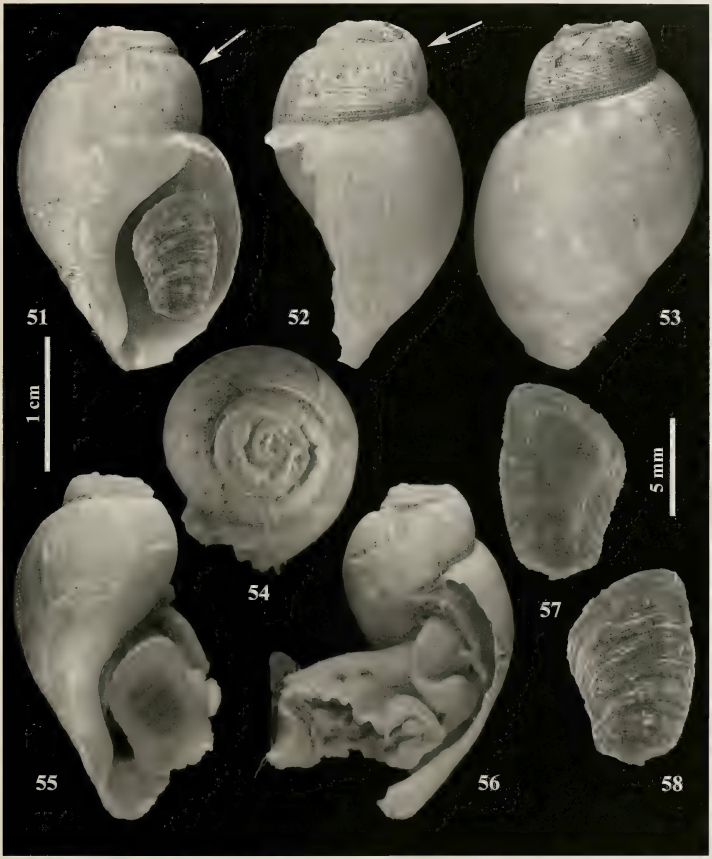
Description: Shell (Figures 51–56) of moderate size (to 26.6 mm), very thin, chalky, ovate, with tapering anterior, eroded spire. Protoconch and upper whorls eroded on all available specimens, with no more than last 2½ whorls remaining. Extrapolation suggests that un-eroded specimens might reach 32 mm, with 5–6 teleoconch whorls. Whorls evenly rounded, with indistinct shoulder, abutting suture. Axial sculpture of fine, sigmoidal, weakly prosocline growth lines, narrower than spiral cords, varying in prominence, producing reticulate pattern in some areas of the shell, especially on penultimate whorl (Figures 51, 52, arrows). Spiral sculpture of fine, sharp, uniform, evenly spaced cords (43–50 on final whorl, 18–21 on penultimate whorl), weaker, more broadly spaced between suture and shoulder as well as near siphon. Aperture large (AL/SL = 0.64–0.71 when using length of eroded shell; AL/SL = 0.54–0.60 as estimated by linear projection of apex), elongate, ovate, tapering anteriorly, deflected from shell axis by 17–18°. Outer lip very thin, not reflected, evenly round from suture to siphonal notch. Inner lip of broad parietal region, shorter, nonaxial columellar region, long siphonal fold and short, broad, axial siphonal canal. Parietal callus consisting of thin glaze, slightly broader posteriorly, narrower or indented near siphonal fold, may form barely perceptible pseudo-umbilicus-like indentation. Shell color uniformly white. Periostracum of very thin axial blades, straw yellow in color. Operculum (Figures 57–58) large, spanning ~0.56 AL, translucent amber yellow in color, with distinctive, claw-like shape, tapering toward nucleus, which is eroded. Outer surface with numerous growth lines nearly perpendicular to long axis. Inner surface with outer rim slightly thickened, glazed, except for long, narrow, triangular attachment area.

Anatomy (Holotype): Body (Figures 65–66) comprises approximately 2½ whorls. Mantle cavity spans ~⅓ whorl, mantle edge thin, does not cover head or penis base. Nephridium very narrow (Figure 65, nep), spans <1/6 whorl, brown-grey. Border between mantle cavity and nephridium marked by deep cleft. Digestive gland (Figures 65, 66, dg) spans 1½ whorl, overlain by testis. Columellar muscle very short, spanning <1 whorl, broad, attached to shell anterior at rear of mantle cavity. Foot large, narrowly oval (L/W ~2.3 for holotype, up to 2.8 in other specimens), not folded during fixation. Body light yellowish, without pigmentation. Head large, with broad, tapering cylindrical tentacles (Figure 65, 66, tn) lacking eyes.

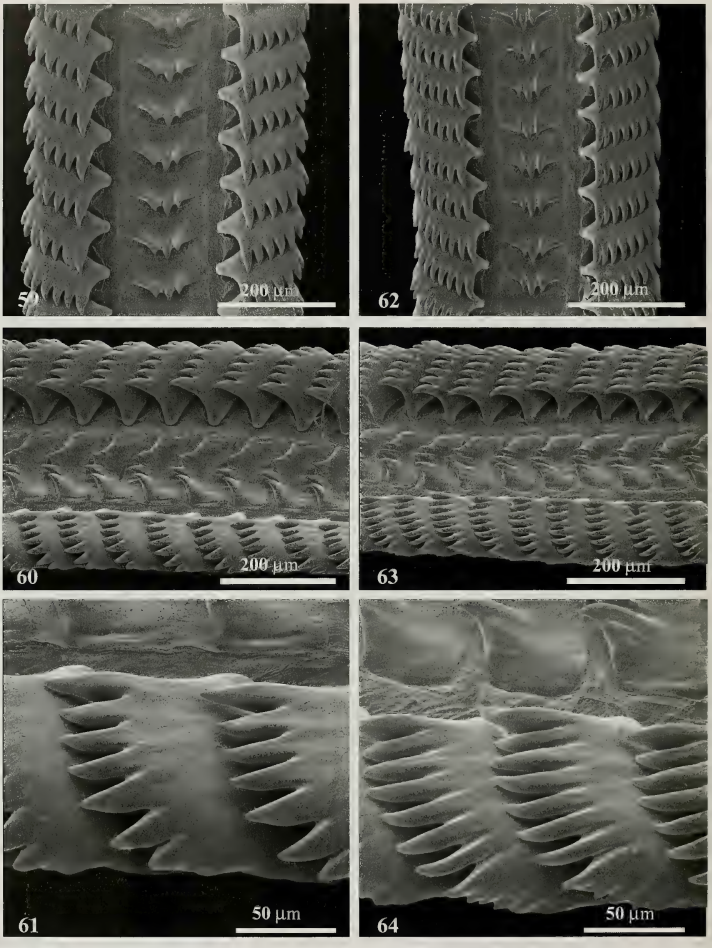
Mantle Cavity (Figure 67): Mantle cavity short, broad (L/W ~0.63). Siphon very short, thin, weakly muscular, extending slightly beyond mantle edge. Osphradium (Figure 67, os) greenish, bipectinate, with broadly curved axis, spanning < 0.4 mantle cavity length. Ctenidium (Figure 67, ct) large, narrower than osphradium, strongly curved, spanning ⅔ mantle cavity length. Hypobranchial gland formed of numerous, indistinct, closely spaced oblique folds covered by thick layer of mucus that partly overlays the rectum.

Alimentary System (Figures 70–75): Proboscis (Figure 71, pr) short (~0.46 AL in holotype), thick, smooth-walled, non-pigmented, not coiled, occupies entire cephalic haemocoel. Proboscis sheath extremely thin-walled, anterior half translucent, thicker posteriorly, but <½ thickness of proboscis wall. Mouth opening (Figure 73) rounded, lumen of buccal tube triangular immediately posterior to mouth. Buccal mass muscular, medium-sized, slightly shorter than retracted proboscis. Odontophoral cartilages paired, fused anteriorly, spanning nearly entire length of buccal mass. Radular ribbon slightly longer than cartilages (~0.30 AL in holotype), ~480 μm wide (holotype), triserial (Figures 59–64), consisting of about 70 (holotype) to 85 (paratype 1) rows of teeth, posteriormost 5 teeth nascent. Oldest several rows of teeth with dark brown pigment that faded when radula cleaned with bleach (NaOCl). Rachidian teeth with broad, rectangular, slightly arched base with straight lateral sides, 3 large, robust, closely spaced cusps. Central cusp slightly longer than lateral cusps. Lateral teeth as broad as rachidian teeth, roughly rectangular, with 7–8 cusps nearly equal in length, outermost cusp shortest, stouter than others, weakly (Figure 61) to strongly (Figure 64) serrated along outer margin. Salivary glands (Figures 70–72, sg) large in comparison to proboscis, acinous, yellowish, fused ventrally, dorsal to oesophagus. Right salivary gland covers valve of Leiblein (Figure 70, vL), part of nerve ring and anterior of proboscis. Left salivary gland shifted posteriorly. Salivary glands tightly attached to proboscis sheath by connective tissue. Salivary ducts (Figures 70, 72, sd) thick, free along both sides of oesophagus, becoming embedded in oesophagus walls shortly after entering retracted proboscis. Valve of Leiblein (Figures 70, 72, 74, vL) well defined, large, pyriform, with ciliary cone, yellow, slightly darker than other organs of cephalic haemocoel. Gland of Leiblein (Figures 70–72, 74, gL) long, dark grey, narrowly tubular, glandular, highly coiled, covered by connective tissue sheath, opens into middle oesophagus posterior to nerve ring via short, narrow duct (Figure 74, dgL). Oesophagus muscular, nearly constant in diameter along most of its length, does not widen before opening into stomach. Stomach (Figure 75) very small, broadly U-shaped, lacks posterior mixing area. Preservation was inadequate to document internal morphology of stomach. Rectum (Figure 67, re) short, narrow, thin-walled, with terminal papilla, spans slightly more than half the length of mantle cavity.

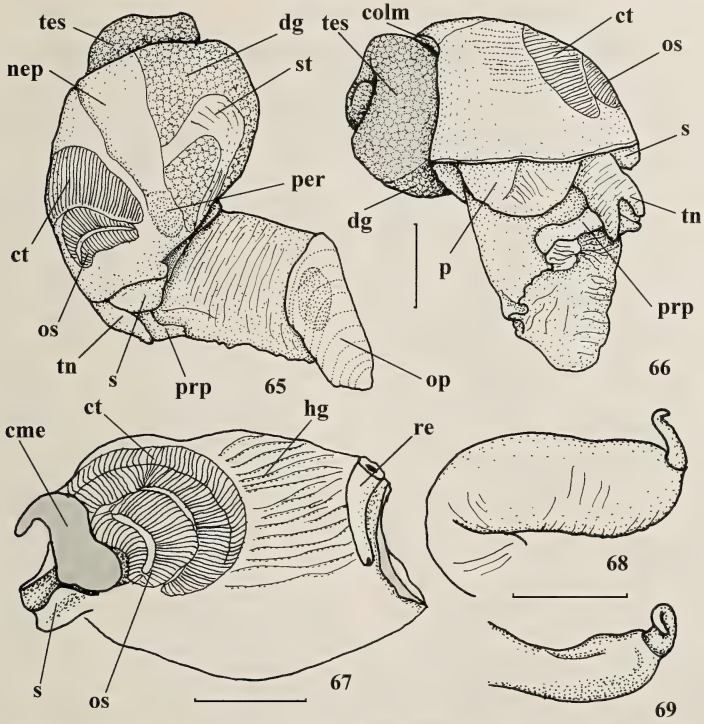
Male Reproductive System: Holotype, Paratypes 1 and 2, males. Testis large, anterior margin at posteriormost part of stomach extends posteriorly along digestive gland for 1½ whorls. Testis similar in color and texture to digestive gland. Seminal vesicle small, formed of very few loops. Penis (Figures 66, p; 68, 69) non-pigmented, spans entire length of mantle cavity, flattened in middle



Figures 51–58. Shells and operculum of *Muffinbuccinum catherinae* new species. **51.** Apertural, **52.** lateral, **53.** dorsal, and **54.** apical views of the holotype, USNM 1010623, South Atlantic Ocean [Argentine Abyssal Plain], 47°17.3′ S, 47°45.7′ W, in 5685–5798 m [R/V Islas Orcadas Cruise 575, Sta. 4]. **55.** Apertural, and **56.** lateral views of the shell of Paratype 1, USNM 1010624, from the type locality. **57.** Inner, and **58.** outer views of operculum of holotype. Arrows indicate regions of finely reticulate surface sculpture.



Figures 59–64. Radulae of *Muffinbuccinum catherinae* new species. **59–61.** Paratype 1. **62–64.** Holotype. **59, 62.** Dorsal, and **60, 63.** right lateral (45°) views of the central portion of the radular ribbon. **61, 64.** Enlarged right lateral views of lateral teeth showing the denticles along the outer cusp.



Figures 65–69. Anatomy of *Muffinbuccinum catherinae* new species, holotype. **65.** Left, and **66.** right lateral views of animal removed from shell. **67.** Mantle cavity organs. **68.** Dorsal, and **69.** right lateral views of the penis. Scale bars = 5 mm. **cme,** cut mantle edge; **colm,** columellar muscle; **ct,** ctenidium; **dg,** digestive gland; **hg,** hypobranchial gland; **nep,** nephridium; **op,** operculum; **os,** osphradium; **p,** penis; **per,** pericardium; **prp,** propodium; **re,** rectum; **s,** siphon; **st,** stomach; **tes,** testis; **tn,** cephalic tentacles.

part, widens anteriorly. Long, cylindrical papilla at distal end of penis surrounded by circular fold around its base.

Type Locality: South Atlantic Ocean [Argentine Abyssal Plain], 47°17.3′ S, 47°45.7′ W, in 5685–5798 m. [R/V Islas Orcadas Cruise 575, Sta. 4, 8 May 1975].

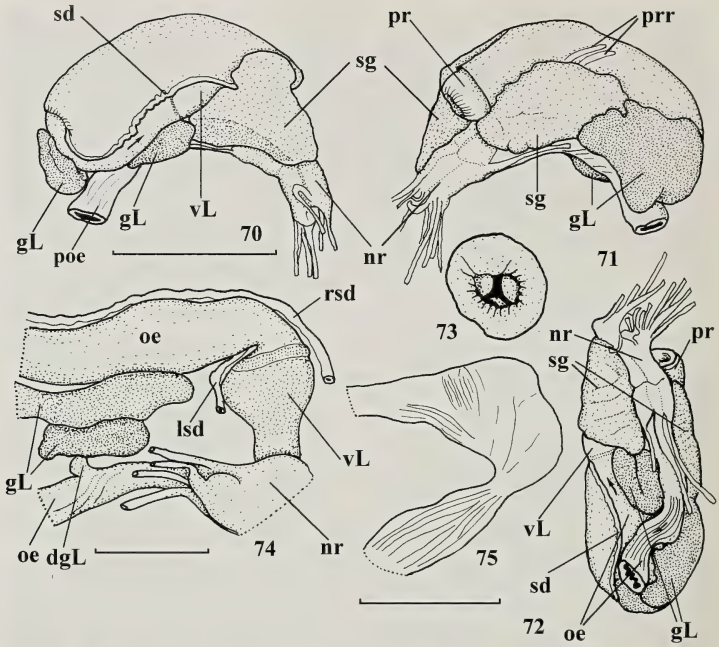
Type Material: Holotype, ♂, USNM 1010623; Paratype 1, ♂, shell partially broken, Paratype 2, ♂, shell fragmented, USNM 1010624, all from the type locality.

Other Material Examined: USNM 1010625, fragments and soft tissues of 3 specimens from the type locality. One was dissected to illustrate the anatomy of the anterior foregut.

Distribution (Figure 76): This species is known only from the type locality, the Argentine Abyssal Plain, off the northern slope of the Falkland Plateau, at depths of 5685–5798 m.

Etymology: This species is named for the senior author's younger daughter, Catherine Laura Harasewych.

Remarks: Of the Antarctic buccinoideans, this new species appears conchologically most similar to *Spike-*



Figures 70–75. Digestive system of *Muffinbuccinum catherinae* new species. **70–74.** Female specimen without a shell, USNM 1010625. **75.** Holotype. **70.** Left lateral, **71.** right lateral, and **72.** ventral views of anterior alimentary system. **73.** Anterior view of the proboscis tip. **74.** Right lateral view of the anterior oesophagus showing the opening of the duct of gland of Leiblein and valve of Leiblein. Salivary glands removed. **75.** Dorsal view of stomach. Scale bars = 5 mm for Figures 70–73, 75, and 2 mm for Figure 74. **dgL,** duct of gland of Leiblein; **gL,** gland of Leiblein; **lsd,** duct of left salivary gland; **nr,** circumoesophageal nerve ring; **oe,** oesophagus; **poe,** posterior oesophagus; **pr,** proboscis; **prr,** proboscis retractors; **rsd,** duct of right salivary gland; **sd,** salivary duct; **sg,** salivary gland; **vL,** valve of Leiblein.

buccinum stephaniae and, to a lesser extent, to *Chlanidota* (*Pfefferia*) *invenusta*. It differs from both in having a more elongated shell, with a long siphonal fold and a short, broad, anteriorly rounded siphonal canal. The surface sculpture of *Muffinbuccinum catherinae* is finer, and the occasional, weak reticulate sculpture of *Muffinbuccinum* is absent in *Spikebuccinum* and *Chlanidota*.

The distinctive radular morphology of *Muffinbuccinum catherinae,* with its broad, tricuspid rachidian and pectinate lateral teeth, readily distinguishes this species from other buccinoidean taxa. Based on the morphology of the radula, *Muffinbuccinum catherinae* appears to be related to *Proneptunea* Thiele, 1912 (Thiele, 1904, pl. 9, fig. 58; Powell, 1951, fig. K 66–67), a circumantarctic genus that occurs from sublittoral (*Proneptunea fenestrata* Powell, 1951, 17–27 m) to bathyal (*Proneptunea rossiana* Dell, 1990, 369–870 m) depths. *Muffinbuccinum* and *Proneptunea* both have tricuspid rachidian teeth and multicuspid lateral teeth that may bear serrations along their outer edge. However, the rachidian teeth of *Muffinbuccinum* are as broad as the lateral teeth, shorter than wide, and have the cusps concentrated in the middle portion of the tooth, while the rachidian teeth of species of *Proneptunea* are narrower, with the three cusps spanning much or their width. The longest and most prominent of the 7–8 cusps on the lateral teeth of *Muffinbuccinum* is the innermost cusp, while the largest and most prominent of the 5 cusps on the lateral teeth

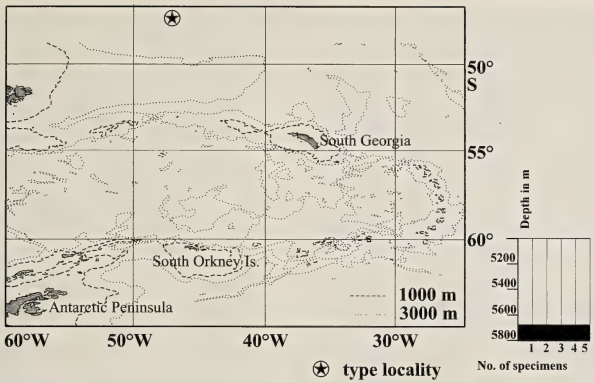


Figure 76. Geographic and bathymetric distribution of *Muffinbuccinum catherinae* new species.

of the 3 (of 6) species of *Proneptunea* for which the radular morphology is known, is invariably the outermost cusp. Based on the presence of a tricuspid rachidian and multicuspid lateral teeth serrated along their outer edge in *Muffinbuccinum,* and their overall resemblance to the radulae of *Proneptunea,* we include *Muffinbuccinum* in the subfamily Prosiphiinae.

Similarities also exist between *Muffinbuccinum catherinae* and several bathyal, abyssal, and hadal buccinoideans of uncertain affinities, notably *Callioncha* Lus, 1978, *Costaria* Golikov, 1977, *Thalassoplanes* Dall, 1908, and *Troschelia* Mörch, 1876. The radula of *Callioncha* [as *Callioconcha*] *knudseni* Bouchet and Warén, 1986 (Bouchet and Warén, 1986: fig. 1), a species from the Kermadec Trench (in 5480 m) resembles that of *Muffinbuccinum catherinae* in having a tricuspid rachidian tooth that is nearly as broad as the lateral teeth, and lateral teeth with 5 cusps of equal length, but lacking serrations along their outer margin. Bouchet and Warén (1986:484) noted similarities in the radulae of *Bayerius* Olsson, 1971 [Olsson, 1971: fig. 101 for *B. fragilissimus* (Dall, 1908) (type species), and Warén and Bouchet, 2001: figs. 39b,c) for *B. arnoldi* (Lus, 1981) and *B. peruvianus* Warén and Bouchet, 2001, respectively] and *Callioncha* Lus, 1978 [Lus, 1978: figs. 2 (7–10) for *C. solida* Lus, 1978 (type species), and Lus, 1989: figs. 5 (1–2) for *C. iturupi* Lus, 1989], and speculated that these genera may prove to be synonyms. However, the type species of *Callioncha,* which dwells in the Izu-Bonin Trench (6770 m), *C. iturupi,* from the Kurile-Kamchatka Trench (8240 m), *Bayerius fragillisimus* (Dall, 1908), known from off Panama and Ecuador (2877–3200 m), *B. arnoldi,* from the Japan, Kuril, and Aleutian Trenches (4800–6135 m), and *B. peruvianus* from 5385–5996 m off Peru all share tricuspid lateral teeth that differ in dentition and proportion from those of *Calli-*

Table 3. *Muffinbuccinum catherinae* new species. Measurements of shell characters of Holotype and Paratype 1. Paratype 2, fragmented. Linear measurements in mm.

Character	Holotype	Paratype 1
Shell length (SL)	26.4	26.6
Final whorl length (FWL)	24.6	23.7
Aperture length (AL)	19.1	20.8
Siphonal canal length (SCL)	2.4	3.6
Shell width (SW)	16.3	15.6
FWL/SL	0.93	0.89
AL/SL	0.72	0.78
SCL/SL	0.09	0.14
SW/SL	0.62	0.59
Number of spiral cords on penultimate whorl	18	21
Number of spiral cords on final whorl	43	50

loncha knudseni. While *Calliloncha* may prove to be a synonym of *Bayerius*, it seems unlikely that *C. knudseni* is referable to this genus. The radulae of *Costaria* (Bouchet and Warén, 1986: fig. 6), *Thalassoplanes* (Bouchet and Warén, 1986: fig. 5) and *Troschelia* (Bouchet and Warén, 1985: figs. 484–485) all have lateral teeth that are roughly rectangular and multicuspid. However, these three genera have rachidian teeth that are very narrow. In *Costaria* and *Thalassoplanes* the central of three cusps may be reduced or absent, while in *Troschelia* the flanking cusps are absent, resulting in monocuspid rachidian teeth.

The operculum of *Muffinbuccinum catherinae* is rather distinctive in being claw-shaped, with growth lines nearly perpendicular to the long axis, and a long, narrow, triangular attachment area along its inner surface. A survey of the literature shows that this operculum type also occurs in *Proneptunea fenestrata* (Powell, 1951: fig. N124), as well as in *Thalassoplanes moerchi* (Bouchet and Warén, 1986: fig. 25), *Calliloncha knudseni* (Bouchet and Warén, 1986: fig. 32), but not *C. solida*, the type of the genus, (Lus, 1978: fig. 2, 4–5) both from the abyssal to hadal zones of the Pacific Ocean, and in *Liomesus ovum* (Turton, 1825) (Bouchet and Warén, 1985: fig. 440) a North Atlantic species inhabiting outer continental shelf depths. *Muffinbuccinum catherinae* co-occurs with *Drepanodontus tatyanae* new genus, new species (see above).

Germonea new genus

Type Species: *Germonea rachelae* new species, by original designation.

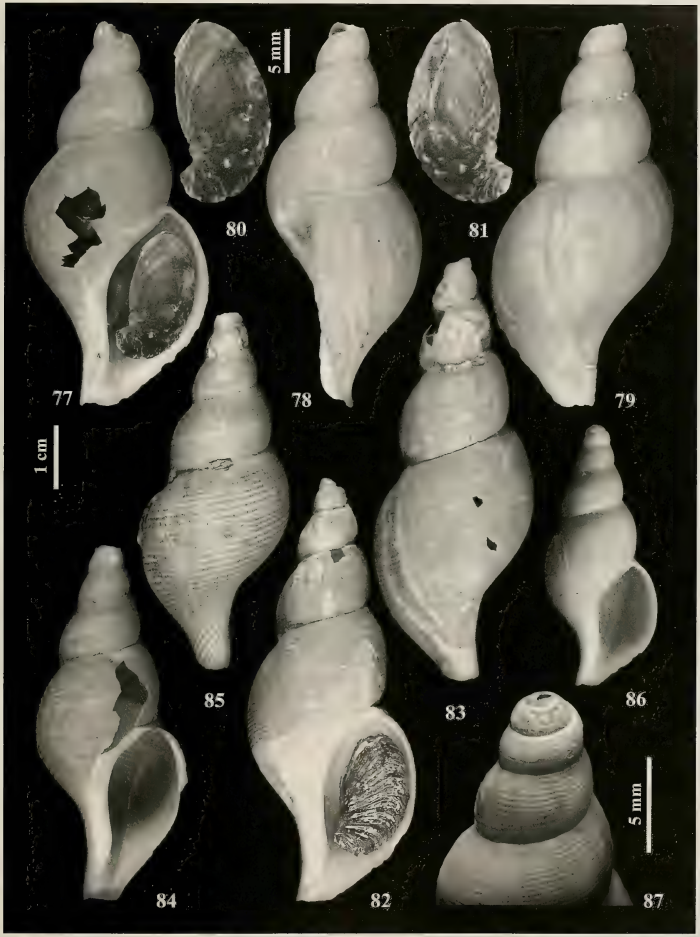
Description: Protoconch large (to 4.4 mm), of ~2⅓ whorls, first 2 whorls smooth, rounded, followed by onset broad, rounded spiral cords. Transition to teleoconch distinct, marked by axial indentation, change in shell color. Teleoconch large (to 67.8 mm), of up to 5 smooth, evenly ovate whorls, with indistinct shoulder, abutting suture. Axial sculpture of fine growth lines, irregular rugae near suture. Spiral sculpture of closely spaced cords. Aperture large, narrowly elliptical, with short, broad, siphonal canal. Outer lip may be slightly reflected, thickened along margin. Inner lip with glossy parietal callus, long columella, siphonal fold. Neither siphonal fasciole, nor pseudoumbilicus present. Periostracum thin, tightly adherent. Operculum large (~0.65 AL), long, narrow, with terminal nucleus at end of strongly curved anterior margin. Columellar muscle very short (~½ whorl). Foot with deep propodial cleft. Head large, with short neck, large black eyes at base of broad, tapering tentacles. Buccal mass large, filling proboscis. Odontophore shorter, radula longer than buccal mass. Rachidian teeth long, narrow (L/W ~2.5), Y-shaped, with 3 stout, radially oriented cusps, central cusp longest. Lateral teeth with 3–4 cusps of similar length along innermost ⅔ of basal plate. Salivary glands large, right larger than left. Gland of Leiblein large, ascinous. Oesophagus thick, broad. Stomach U-shaped, lacking posterior mixing area.

Etymology: The genus is named after Mrs. Rachel (Raye) N. Germon, in recognition of her years of work in managing the collections of Antarctic Mollusca at the National Museum of Natural History, Smithsonian Institution.

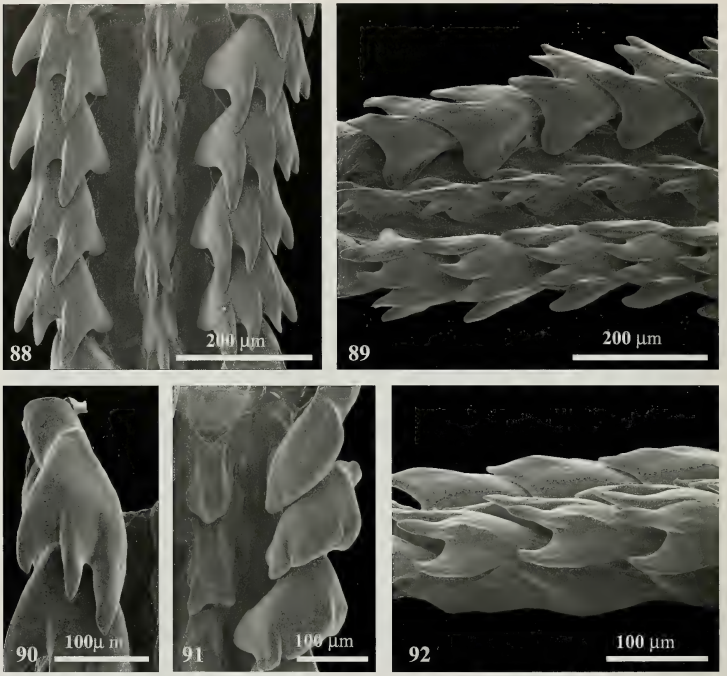
Germonea rachelae new species
(Figures 77–98, Table 4)

Description: Shell (Figures 77–79, 82–86) large (to 67.8 mm), thin to moderately thick, fusiform. Protoconch (Figure 87) increasing from 1.1 mm to 4.4 mm in diameter in ~2⅓ whorls, first 2 whorls smooth, rounded, followed by onset of weak, broad, rounded spiral cords. Transition to teleoconch marked by distinct axial indentation, change in shell color, with axial growth lines, spiral cords markedly more prominent. Teleoconch of up to 5 smooth, evenly ovate whorls, with indistinct shoulder, abutting suture. Axial sculpture limited to fine, straight, weakly prosocline growth lines, some more pronounced, giving rise to irregularly spaced, weak surface rugae near suture. Spiral sculpture of numerous (18–30 on penultimate whorl; 48–81 on last whorl), closely spaced cords, broader than intervening spaces. Finer threads may occur between adjacent cords, especially along anterior portion of final whorl. Aperture large (AL/SL = 0.49–0.57), narrowly elliptical, deflected from shell axis by 14–17°. Siphonal canal short (~¼ aperture length), broad, open, crosses shell axis. Outer lip may be slightly reflected, weakly thickened along margin, evenly rounded from suture to base of siphonal canal. Inner lip of short, weakly convex parietal region, long, slightly concave columella, long siphonal fold extending beyond narrow glossy parietal callus. Neither siphonal fasciole, nor pseudoumbilicus present. Protoconch ivory colored, teleoconch uniformly white, aperture, parietal callus glossy. Periostracum amber yellow to brown, tightly adherent to shell. Operculum (Figures 80, 81) large (~0.65 AL), translucent yellow to amber in color, long, narrow, with terminal nucleus at end of strongly curved anterior margin. Outer surface of operculum with fine, regular growth lines. Inner surface with small, oval attachment area along posterior, adaxial region, broad, strongly thickened, heavily glazed free outer and anterior margins.

Anatomy (Holotype): Based on rehydrated animal, soft tissues (lacking upper part of kidney, digestive gland) comprise approximately 1½ whorl. Mantle cavity spans <⅓ whorl, mantle edge thick, does not cover head or base of penis. Columellar muscle very short, comprising ~½ whorl. Foot of medium size, strongly contracted, broadly oval (L/W ~1.4), with narrow propodium separated by deep propodial cleft. Body yellowish tan, non-pigmented. Head large, with short neck, broad, tapering tentacles, large black eyes at base of tentacles.



Figures 77–87. Shells and opercula of *Germonea rachelae* new species. **77.** Apertural, **78.** Lateral, and **79.** dorsal views of the holotype, USNM 896594, off South Georgia Island, 58°02′ S, 37°57′ W, in 3197–3239 m [R/V Eltanin cruise 9, sta. 698]. **80.** Outer and **81.** Inner views of the operculum of the holotype. **82.** Apertural and **83.** Dorsal views of paratype 1, USNM 1010620. N of South Orkney Islands, 58°06′ S, 44°56′ W, in 2800 m [R/V Eltanin, cruise 7, sta. 480]. **84.** Apertural and **85.** dorsal views of paratype 2, USNM 898828, off South Georgia Island, 55°02′ S, 44°21′ W, in 3623–3714 m [R/V Eltanin cruise 7, sta. 469]. **86.** Apertural and **87.** apical views of paratype 3, USNM 1010621, off South Georgia Island, 54°59′ S, 38°13′ W, in 2379–2196 m [R/V Eltanin, cruise 9, sta. 686].

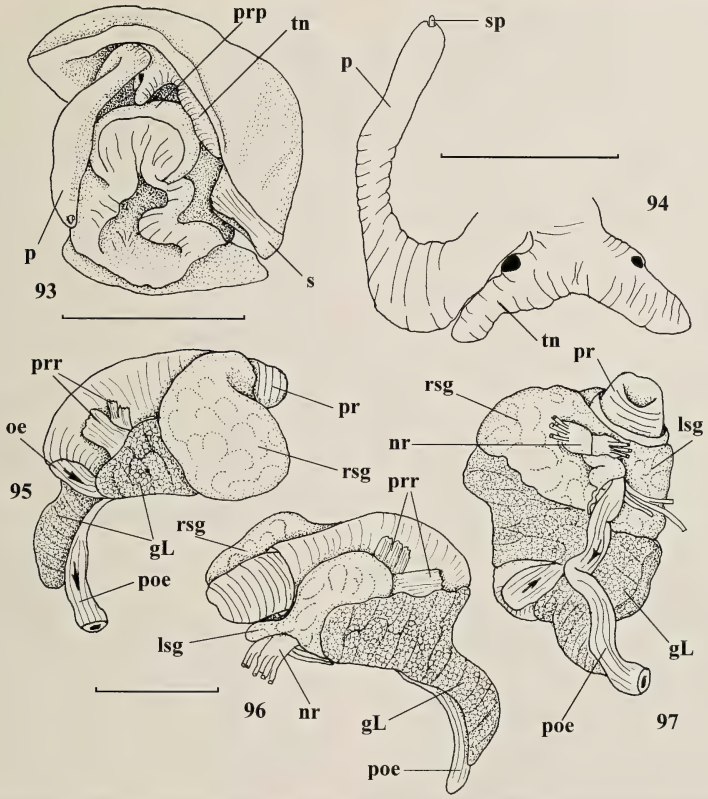


Figures 88–92. Radula of holotype of *Germonea rachelae* new species. **88.** Dorsal, and **89.** right lateral (45°) views of the central portion of the radular ribbon. **90.** Single lateral tooth (partially broken) to show concentration of cusps along inner portion of basal plate. **91.** Dorsal view of the bending plane, showing worn teeth. **92.** Right lateral (75°) view of the central portion of the radular ribbon.

Siphon very short, free, muscular, extends slightly beyond mantle edge.

Mantle Cavity: Mantle of female specimen, although damaged, was partially present. Mantle of moderate width (L/W ~0.8), very thin, mantle edge evenly thickened. Osphradium yellowish, bipectinate, symmetrical, narrow, spanning ~0.7 mantle cavity length. Ctenidium equal in width to osphradium, slightly longer, curved. Lamellae uniform in shape along entire ctenidium length, tall, triangular, with short curved tip, similar to that in posterior part of *Lusitromina abyssorum* (Lus, 1993) (Figure 129). Hypobranchial gland poorly developed, lacks distinct folds. Rectum spans ~⅔ mantle cavity length, with terminal anus, distinct anal papilla.

Alimentary System (Figures 95–97): Proboscis (Figures 95, 97, pr) short when retracted (~0.30 AL), narrow (L/D ~4.0), with folded walls, non-pigmented. Proboscis retractors (Figures 95, 96, prr) powerful, arranged in symmetrical bundles attached to posterior part of proboscis sheath when proboscis retracted. Anterior ⅔ of proboscis sheath very thin-walled, translucent, thickening posteriorly until as thick as proboscis wall, which comprises ~0.1 proboscis diameter. Mouth opening triangular slit. Buccal mass muscular, large, filling, but not extending beyond retracted proboscis. Odontophoral cartilages paired, fused anteriorly, ~¾ of buccal mass length. Radular ribbon of holotype (Figures 88–92) longer than proboscis (14 mm, 0.42 AL), narrow, (~420 µm), triserial, consisting of 110 rows, anteriormost 28



Figures 93–97. Anatomy of *Germonea rachelae* new species. **93–94.** Holotype, male. **95–97.** Female, [R/V Eltanin, sta. 695]. **93.** Anterior view of animal. **94.** Head and penis. **95.** Right lateral, **96.** left lateral, and **97.** ventral views of anterior alimentary system. Scale bars = 5 mm. **gL,** gland of Leiblein; **lsg,** left salivary gland; **nr,** circumoesophageal nerve ring; **oe,** oesophagus; **p,** penis; **poe,** posterior oesophagus; **pr,** proboscis; **prp,** propodium; **prr,** proboscis retractors; **rsg,** right salivary gland; **s,** siphon; **sp,** seminal papilla; **tn,** cephalic tentacles.

rows below bending plane in sublingual pouch, posteriormost 7 rows nascent. Radula strongly sclerotized, dark yellow. Rachidian teeth (Figures 88, 89) long (~185 μm), very narrow (~75 μm), with anteriorly arched, laterally indented basal plate, 3 stout, radially oriented cusps, central cusp longest. Lateral teeth (Figures 90–92) with long, stout basal plates attached at acute angle (~22–28°) to axis of radular ribbon, with 3–4 robust, roughly parallel cusps of similar length emanating from innermost ~⅔ of basal plate, outermost ~⅓ of basal plate beneath cusps of adjacent lateral tooth. Teeth along bending plane (Figure 91) badly worn. Salivary glands (Figures 95–97, rsg, lsg) large, seemingly fused, acinous. Right salivary gland (Figures 95, 97, rsg) completely cov-

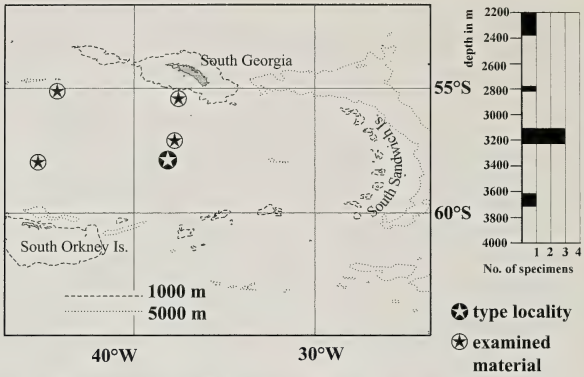


Figure 98. Geographic and bathymetric distributions of *Germonea rachelae* new species.

ers valve of Leiblein, lies dorsal to nerve ring, flanks right, ventral, anterior part of proboscis sheath. Left salivary gland (Figures 96, 97, lsg) smaller than right. Salivary ducts short, thick, become embedded in esophageal wall shortly after leaving salivary glands. Valve of Leiblein large, well defined, pyriform, brownish in preserved specimens, with ciliary cone, whitish glandular pad visible through walls of valve. Gland of Leiblein (Figures 95, 96, gL) large, bulky, brownish, envelopes proboscis ventro-laterally, extends posteriorly along oesophagus, opens into oesophagus via narrow duct well posterior to small circumoesophageal nerve ring (Figures 96, 97, nr). Anterior, mid-, and posterior oesophagus thick, broad, narrowing slightly when passing through nerve ring. Stomach unknown for holotype. Non-type specimen (♀) had portion of stomach preserved, indicating stomach U-shaped, lacking posterior mixing area.

Male Reproductive System (Figures 93–94): Sperm duct runs anteriorly along right side of body to enter base of long, narrow, nearly cylindrical penis (Figure 94) that extends length of mantle cavity. Seminal papilla (Figure 94, sp) very short, surrounded by circular fold.

Type Locality: Off South Georgia Island, 58°02′ S, 37°57′ W, in 3197–3239 m. [R/V Eltanin cruise 9, sta. 698, 30 Aug, 1963].

Type Material: Holotype, ♂, USNM 896594, from the type locality; Paratype 1, ♂, USNM 1010620, N of South Orkney Islands, 58°06′ S, 44°56′ W, in 2800 m. [R/V Eltanin, cruise 7, sta. 480, 15 Feb 1963]; Paratype 2, USNM 898828, off South Georgia Island, 55°02′ S, 44°21′ W, in 3623–3714 m. [R/V Eltanin cruise 7, sta. 469, 12 Feb 1963]; Paratype 3, USNM 1010621, off South Georgia Island, 54°59′ S, 38°13′ W, in 2379–2196 m. [R/V Eltanin cruise 9, sta. 686, 25 Aug 1963].

Other Material Examined: USNM 1013061, off South Georgia Island, 56°53′ S, 37°33′ W, 3144–3138 m. [R/V Eltanin cruise 9, sta. 695, 28 Aug 1963], 2 frag-

Table 4. *Germonea rachelae* new species. Measurements of shell characters. Linear measurements in mm. (n = 4, including holotype).

Character	Mean	σ	Range	Holotype
Shell length (SL)	57.0	11.1	41.7–67.8	61.8
Final whorl length (FWL)	41.5	8.0	30.2–47.9	46.1
Aperture length (AL)	30.4	5.8	22.2–35.5	35.5
Shell width (SW)	24.7	5.3	18.2–30.3	30.3
FWL/SL	0.73	0.02	0.71–0.75	0.75
AL/SL	0.54	0.03	0.49–0.57	0.57
SW/SL	0.43	0.04	0.40–0.49	0.49
Number of spiral cords on penultimate whorl	24.5	5.2	18–30	30
Number of spiral cords on final whorl	58.0	14.4	48–81	81

mentary bodies (1♀ + 1♂) without shells (anatomy examined).

Distribution (Figure 98): This species is known only from the abyssal plain of the Scotia Sea, at depths of 2196–3714 m.

Etymology: The species is named after Mrs. Rachel (Raye) N. Germon, in recognition of her years of work in managing the collections of Antarctic Mollusca at the National Museum of Natural History, Smithsonian Institution.

Remarks: *Germonea rachelae* may be easily identified by its large, fusiform shell, with short siphonal canal and deep amber periostracum. Of the few Antarctic species that reach comparable size, only *Cavineptunea monstrosa* Powell, 1951, from outer continental shelf depths off South Georgia Island, is superficially similar, but differs in having a unique, cylindrical protoconch with indented apex, a broader aperture, and in lacking the axial rugae of *Germonea* near the suture.

The radula of *Germonea rachelae*, with its narrow, tricuspid rachidian teeth, and lateral teeth in which the 3–4 cusps are concentrated along the inner half of the basal plate, has clear affinities with several genera assigned to the subfamily Prosiphiinae (Appendix 1). It is most similar to the radula of several species of *Prosipho* [i.e., *Prosipho spiralis* Thiele, 1912, Numanami, 1996: figs. 116D–E; *Prosipho crassicostatus* (Melvill and Standen, 1907), see Hain, 1989: pl. 24, fig. 1] and *Anomacme smithi* Strebel, 1905 (Powell, 1951: fig. K57). The shells of these sublittoral to bathyal genera, while similar in general shape and proportion to those of *Gemonea,* rarely exceed 10 mm in length. The rachidian teeth of *Germonea rachelae* are far narrower, more elongated, and deeply indented anteriorly (producing a tooth with a Y-shaped outline) than any species of Prosiphiinae. While the opercula of relatively few Prosiphiinae are illustrated, Numanami (1996: fig. 110) shows the operculum of *Prosipho hunteri* Hedley, 1916 to be elongated, slightly smaller than the aperture, with a round attachment area and a terminal nucleus. The distal, free portion of the operculum, containing the terminal nucleus, is not as strongly curved as it is in *Germonea rachelae.*

Subfamily Cominellinae Gray, 1857
Lusitromina new genus

Type Species: *Tromina abyssorum* Lus, 1993, by original designation.

Description: Protoconch increasing in diameter from 470 μm to 2.2 mm in 2 whorls. First whorl smooth, followed by onset of fine, sharp axial lamellae, then, ½ whorl later, by broad, shallow spiral cords. Transition to teleoconch distinct, marked by onset of coarser sculpture. Teleoconch of moderate size (to 29.2 mm), up to 3½ whorls, with strong shoulder on first 2 whorls, increasingly rounded thereafter. Axial sculpture prominent on protoconch, reduced on first teleoconch whorl, limited to fine growth lines on subsequent whorls. Spiral sculpture of broad cords that increase in number, but decrease in prominence with increasing shell size. Aperture large, ovate, columella long, axial, with short siphonal fold. Neither siphonal fasciole nor pseudoumbilicus present. Periostracum of fine axial lamellae. Operculum D-shaped, paucispiral, large. Eyes absent. Kidney narrow. Foot with pronounced propodium. Buccal mass larger than retracted proboscis. Radula with tricuspid rachidian teeth, with central cusp longer, wider that flanking cusps, basal plate broadly rectangular. Lateral teeth with two long, sharp, curved cusps that join above basal plate. Stomach small, U-shaped, without posterior mixing area. Penis with long, cylindrical papilla surrounded by fold around base.

Etymology: The genus is named after the late Dr. Valentina Lus of the P.P. Shirsov Institute of Oceanology, Russian Academy of Sciences, Moscow, for her work on abyssal and hadal Buccinoidea.

Remarks: Dall (1918) proposed the genus *Tromina* without discussion, designating as type species *Fusus unicarinatus* Philippi, 1868, (from subtidal depths of the Magellanic Province), a taxon that he had previously (Dall, 1902: 536) questionably included in the genus "?*Trophon*". Later, Dall (1919: 336) commented that this genus "has the nucleus [protoconch] of a *Trophon* and is probably related to the austral Trophons, but the soft parts are not known." Later still, Dall (1925: 28, plate 21, fig. 7) illustrated the type species.

Several species from the South Atlantic have since been attributed to the genus *Tromina,* including the sublittoral to bathyal Magellanic species: *T. fenestrata* Powell, 1951, *T. simplex* Powell, 1951, *T. tricarinata* Powell, 1951, and *T. bella* Powell, 1951; the abyssal *T. bella abyssicola* Clarke, 1961, from the Cape Basin off SW Africa, and *T. traversiensis* Clarke, 1961, from off the South Sandwich Islands, and the hadal *T. abyssorum* Lus, 1993, from the Orkney Trench. Clarke (1961, 1962) also recognized, but did not name three additional abyssal taxa, referring to them as *Tromina* a, b, c.

Cernohorsky (1977: 110) was the first to note that *Fusus unicarinatus* Philippi, 1868 was preoccupied by *Fusus unicarinatus* Deshayes, 1835. He considered *Tromina tricarinata* to be conspecific with *F. unicarinatus* Philippi, and suggested that it might serve as a replacement name for the type species. Bouchet and Warén (1985: fig. 328, 330) subsequently illustrated the shell (fig. 328) and radula (fig. 330) of *T. unicarinatus,* confirming Dall's (1919) belief that this taxon was a muricid closely "related to the Austral Trophons." Since the original description of *Tromina tricarinata* includes an illustration of its radula that clearly shows this taxon to be a buccinoidean, it could not serve as a replacement name for a species of muricid.

Dell (1990: 208) reviewed the nomenclatural history of *Tromina* and its type species, and proposed *Tromina dispectata* as a new name for *Fusus unicarinatus* Philippi, 1868, *non* Deshayes, 1835. Recognizing that several

buccinoidean taxa previously described in *Tromina* required a new generic allocation, he proposed the new genus *Falsitromina* (type species: *Tromina bella* Powell, 1951), characterized by a distinctive, complex protoconch morphology, small (to 15 mm) shell, paucispiral operculum, and radula with tricuspid rachidian teeth and lateral teeth with two cusps set close together. In addition to the type species, he included *F. simplex, F. tricarinata, F. fenestrata,* and proposed an additional species *F. powelli,* all from bathyal depths of the Magellanic Province, but did not include or mention Clarke's (1961) abyssal species.

The bathyal genus *Antarctodomus* Dell, 1972 (type species: *Bathydomus thielei* Powell, 1958) shares the unusual protoconch morphology (Numanami, 1996: fig. 96C) and obesely fusiform shell shape (Numanami, 1996: fig. 96A–B) of *Falsitromina,* but differs in reaching a much larger size (to 35 mm, Dell, 1990: 169), in having a triangular, sharply tapering operculum (Arnaud, 1972: fig. 20B), and in having a radula with tricuspid rachidian teeth that have a more narrowly rectangular basal plate with a broadly indented anterior edge, and bicuspid lateral teeth with both cusps appearing blunt and nearly cylindrical (Arnaud, 1972: fig. 20C; Numanami, 1996: fig. 96D).

The new genus *Lusitromina* is proposed to contain the abyssal and hadal taxa that were originally described in *Tromina,* namely *T. abyssicola* Clarke, 1961 (as *T. bella abyssicola*), and *T. abyssorum* Lus, 1993. *Tromina traversiensis* Clarke, 1961, was shown to be a cancellariid of the genus *Iphinopsis* Dall, 1924, by Bouchet and Warén (1985: 261).

Lusitromina shares many of the distinctive features characteristic of both *Falsitromina* and *Antarctodomus,* including the complex protoconch morphology, obesely fusiform shell shape, and radulae with tricuspid rachidian teeth and bicuspid lateral teeth. However, the rounded paucispiral operculum of *Lusitromina* serves to distinguish it from *Antarctodomus,* which has a tapering, triangular operculum. The rachidian teeth of *Lusitromina,* while tricuspid, differ from those of both *Falsitromina* and *Antarctodomus* in have a central cusp that is larger than, rather than equal in size to the flanking cusps. The basal plate of the rachidian tooth is broadly rectangular, intermediate between the squarish basal plate of *Falsitromina,* and the very narrow and deeply indented basal plate of *Antarctodomus.* The lateral teeth of *Lusitromina* have two sharp, curved cusps of equal size that fuse above the basal plate, while the cusps of both *Falsitromina* and *Antarctodomus* are not equal in length or width.

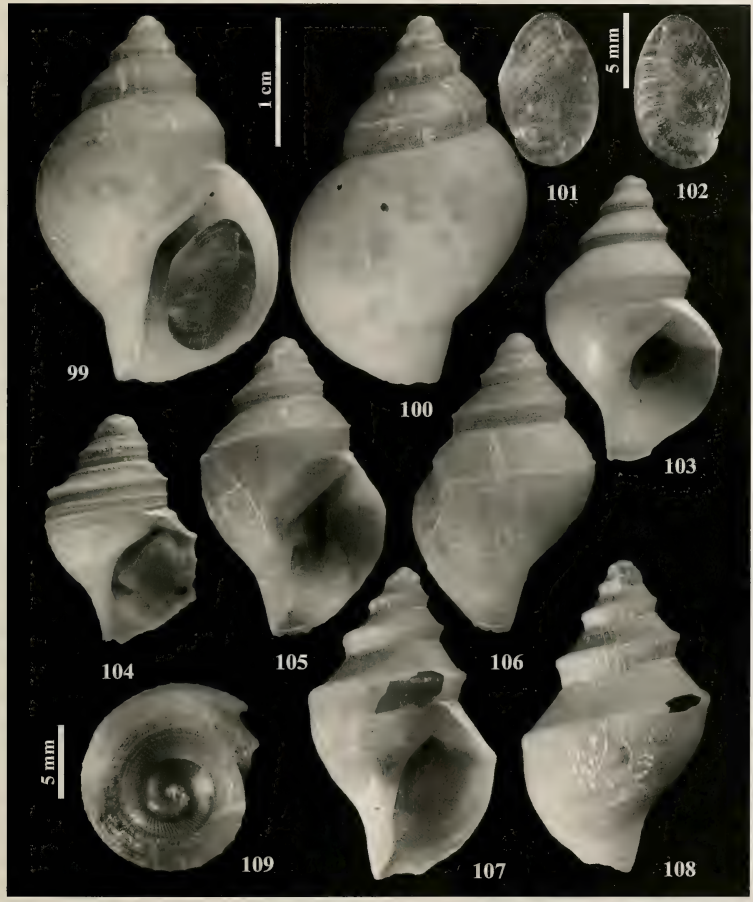
Lusitromina abyssorum (Lus, 1993)
(Figures 99–137, Table 5)

Synonymy—*Tromina abyssorum* Lus, 1993:178

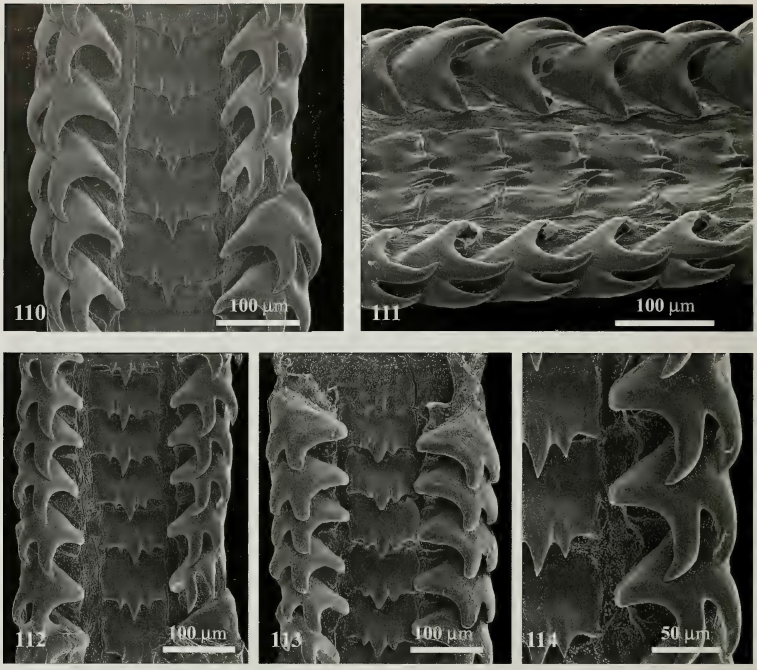
Description: Shell (Figures 99–100, 103–109) of moderate size (to 29.2 mm), thin, small specimens translucent, largest specimens opaque along last whorl. Shell shouldered, biconical when small, ovate when large. Protoconch well preserved, especially in small specimens (Figures 115–117). Protoconch increasing from 470 μm to 2.2 mm in diameter in 2 whorls, first 0.9 whorl smooth, slightly pitted, followed by onset of fine, sharp axial threads, and ½ later, by broader spiral cords. Transition to teleoconch distinct (Figures 116, 117 arrows), followed by onset of coarser axial sculpture. Teleoconch of up to 3½ whorls. Shoulder pronounced on first 2 whorls, marked by thick spiral cord, producing a stepped spire, becoming progressively less conspicuous in subsequent whorls, entirely rounded following third whorl (Figures 99–100). Axial sculpture of strong, evenly spaced cords dominant on protoconch, becoming more widely spaced, less prominent following transition to teleoconch, disappearing entirely after first ½ teleoconch whorl. Subsequent axial sculpture confined to very fine, weakly prosocline growth lines. Spiral sculpture of broad cords that usually increase in number, but decrease in prominence with increasing shell size, 4–20 on penultimate whorl, 2–20 between suture and shoulder, 19–53 on last whorl. Aperture large (AL/SL = 0.62–0.66), broadly oval, deflected from shell axis by 24–27°. Outer lip very thin, not reflected, evenly rounded from shoulder to base of short, broad, axial siphonal canal. Shell composed of three layers (Figure 121), outermost layer (~2 μm) of columnar calcitic crystals, middle layer, thickest (~26 μm) of collabrally oriented crossed-lamellar crystals, innermost layer (~4 μm) of crossed lamellar crystals oriented perpendicular to middle layer. Inner lip of wide, weakly convex parietal region, straight, weakly indented axial columellar region of equal length, with long siphonal fold defining abaxial portion of siphonal canal. Neither siphonal fasciole nor pseudoumbilicus present. Shell color uniformly white. Periostracum (Figure 120) very thin, straw yellow in color, with extremely fine axial lamellae. Operculum (Figures 101–102, 118–119) D-shaped, large, spanning ~0.61 AL, thin, yellowish, broadly ovate, paucispiral, with nucleus near adaxial, abapical edge (Figures 118–119).

Anatomy (Figures 122–124): Soft tissues comprise approximately 3¼ whorls. Mantle cavity spans just under ½ whorl, kidney narrow, spans about 1/7 whorl. Columellar muscle short, comprising slightly less than 1 whorl, attaching to shell at rear of mantle cavity. Foot large, long (L/W ~2.2), with well developed, crescent-shaped propodium. Propodial cleft very wide, containing conspicuous propodial gland with rounded opening (Figures 123, 124, pg). Body color yellowish tan, without pigmentation pattern. Kidney, digestive system, testis all greenish. Head large, with long, conical tentacles (Figure 123, tn), without discernable neck. Eyes absent. Nephridium brown, folds lighter in color, visible through wall. Mantle covers base of head and most of penis. Pericardium (Figure 122, per) ventral to narrow nephridial gland.

Mantle Cavity (Figure 128): Mantle cavity short,



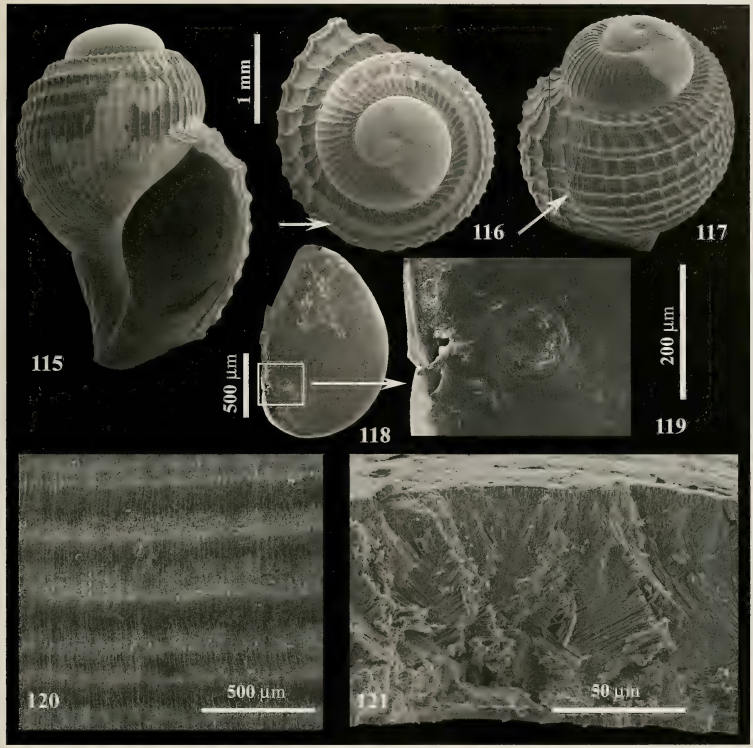
Figures 99–109. Shells and opercula of *Lusitromina abyssorum* (Lus, 1993). **99–102.** USNM 1010536, off Saunders Island, South Sandwich Islands, 57°39′00″ S, 26°00′24″ W, in 2380–2609 m [R/V Islas Orcadas, sta. 54]. **99.** Apertural, and **100.** dorsal views of shell. **101.** Outer, and **102.** inner views of operculum. **103.** Apertural view, USNM 896533, off South Georgia Island, 56°04′ S, 33°59′ W, in 3138–3239 m [R/V Eltanin, sta. 722]. **104.** Apertural view, USNM 896785, N of South Orkney Islands, 60°06′ S, 45°26′ W, depth not recorded (estimated > 5000 m), [R/V Eltanin, sta. 488]. **105.** Apertural and **106.** Dorsal views, USNM 1010535, E of Candlemas Island, South Sandwich Islands, 57°00′24″ S, 26°10′06″ W, in 2740–2757 m [R/V Islas Orcadas, sta. 38]. **107.** Apertural, **108.** dorsal, and **109.** apical views, USNM 896525, N of South Georgia Island, 53°02′ S, 37°40′ W, in 3056–3102 m [R/V Eltanin, sta. 735].



Figures 110–114. Radulae of *Lusitromina abyssorum* (Lus, 1993). **110.** Dorsal, and **111.** Right lateral (30°) views of the central portion of the radular ribbon of specimen in Figures 99–100, USNM 1010536. **112–113.** Dorsal views of the radular ribbon of specimen in Figures 107–109, USNM 896525. **112.** Dorsal view of central portion of radula. **113.** Anteriormost part of radular ribbon, showing worn teeth. **114.** Enlarged right lateral teeth, showing bifurcation of outer cusp.

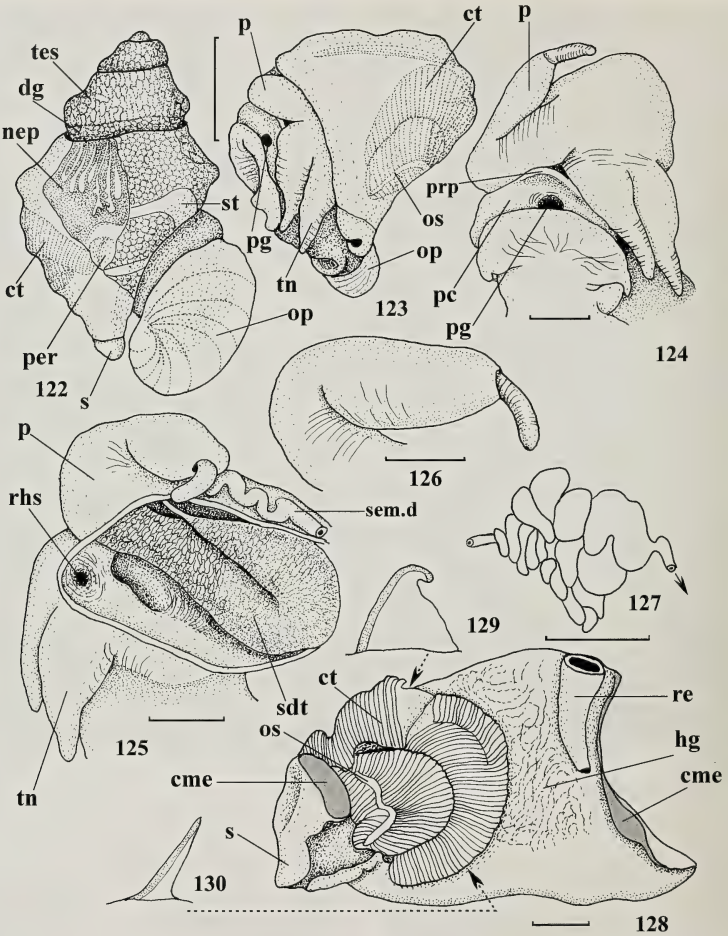
broad (L/W ~0.6). Mantle edge smooth. Siphon very short, broad, muscular, extending slightly beyond mantle edge. Osphradium (Figure 128, os) yellowish, bipectinate, large (~½ mantle cavity length), very wide, with wide, curved osphradial nerve. Ctenidium (Figure 128, ct) large, narrower than osphradium, strongly curved, spanning nearly entire mantle cavity length. Shape of ctenidium lamellae varies with position along organ. Lamellae tall, triangular posteriorly (Figure 129), gradually becoming narrower anteriorly (Figure 130). Hypobranchial gland without distinct folds, covered by thick layer of mucus. Rectum short, spans <½ mantle cavity length. Anus terminal, without papilla.

Alimentary System (Figures 131–136): Proboscis (133, pr) short when retracted (~0.36 AL), not thick (L/D ~3.3), smooth, non-pigmented. Proboscis retractors (Figures 133, 134, prr) not numerous, but thick, powerful, attached to proboscis sheath at mid-length, when proboscis retracted. Proboscis sheath very thin-walled, anterior half translucent, thickened posteriorly to become as thick as proboscis wall. Proboscis wall thin ~1/10 proboscis diameter. Mouth opening triangular slit. Buccal mass muscular, large, filling retracted proboscis, slightly protruding from its posterior end (Figure 136, bm). Odontophoral cartilages paired, fused anteriorly, but connected only by very thin layer of tissue, comprise ~¾ of buccal mass length. Radular ribbon equal in length to retracted proboscis (4.3–5.0 mm, 0.26–0.28 AL), 300–330 µm wide, triserial (Figures 110–114), with 65–76 rows of teeth, posteriormost 5–6 rows

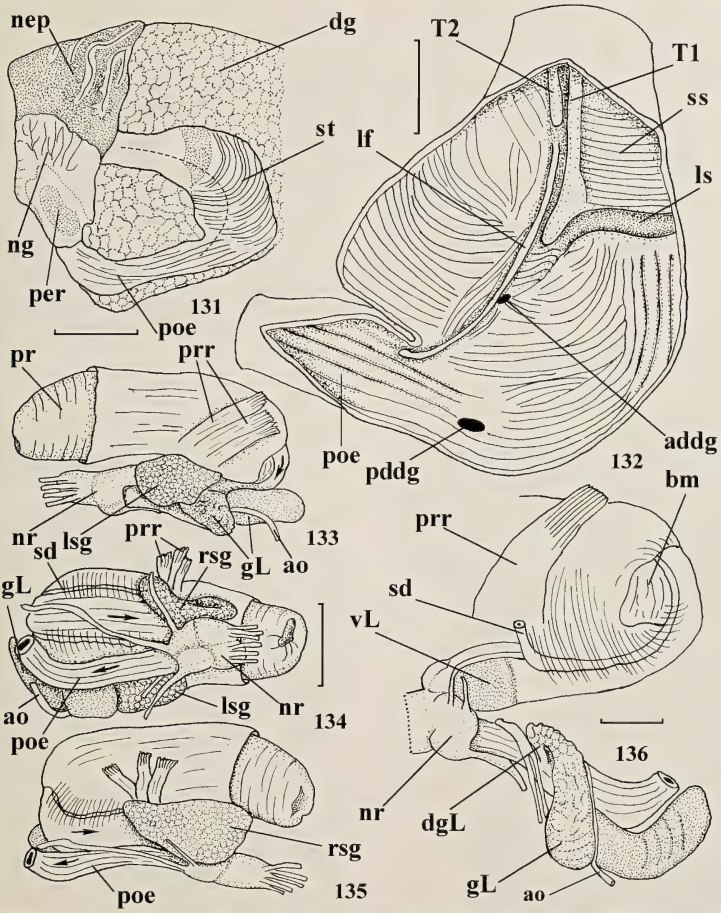


Figures 115–121. *Lusitromina abyssorum* (Lus, 1993). **115.** Apertural, **116.** apical, and **117.** latero-dorsal views of the shell of a juvenile specimen, USNM 896800, Scotia Ridge, 56°02′ S, 61°56′ W, in 4008 m, [R/V *Eltanin*, sta. 112]. Arrows indicate transition from protoconch to teleoconch. **118–119.** Operculum of the same specimen. **118.** Outer surface of operculum. **119.** Enlarged nucleus of operculum. **120.** Periostracum, and **121.** shell ultrastructure of specimen shown in Figures 107–109, USNM 896525.

nascent. Rachidian teeth with 3 cusps on posterior portion of broad, anteriorly arched basal plate. Central cusp slightly longer, wider than lateral cusps. Lateral teeth with 2 cusps of approximately equal length. Outer cusp with bifurcated tip in one specimen (Figure 114). Salivary glands (Figures 133–135, lsg, rsg) small, not fused, acinous. Right salivary gland completely covers valve of Leiblein, lies dorsally to the nervous ring (Figures 134, 135, rsg). Left salivary gland more rounded, situated laterally, just posterior to the nerve ring (Figure 133, 134, lsg). Salivary ducts (Figure 134, 136, sd) short, thick, become embedded in oesophageal wall shortly after leaving the gland. Valve of Leiblein (Figure 136, vL) well defined, large, pyriform, with ciliary cone, whitish glandular pad visible through walls of valve. Gland of Leiblein (Figures 133, 134, 136, gL) small, yellowish, short, tubular, not coiled, opening into oesophagus via short duct (Figure 136, dgL) slightly posterior to the nerve ring. Oesophagus thick, broad anterior to nerve ring, narrower posterior to nerve ring (Figures 134, 135, poe), does not widen before entering stomach (Figures 131, 132, poe). Stomach (Figures 131, st; 132) small, U-



Figures 122–130. Anatomy of *Lusitromina abyssorum* (Lus, 1993), specimen shown in Figures 107–109, USNM 896525. **122–123.** Lateral views of the animal removed from shell. **124.** Anterior view of the foot showing the pedal gland. **125.** Cephalic haemocoel, with organs of the digestive system removed to show the enlarged seminal duct. **126.** Dorsal view of penis. **127.** Seminal vesicle. **128.** Mantle cavity organs. **129–130.** Shape of ctenidium lanellae in different regions of ctenidium. Scale bars = 2 mm. **cme,** cut mantle edge; **ct,** ctenidium; **dg,** digestive gland; **hg,** hypobranchial gland; **nep,** nephridium; **op,** operculum; **os,** osphradium; **p,** penis; **pc,** propodium; **per,** pericardium; **pg,** propodial gland; **re,** rectum; **rhs,** rhynchostome; **s,** siphon; **sdt,** glandular seminal duct (prostate gland); **sem.d,** seminal duct; **st,** stomach; **tes,** testis; **tn,** cephalic tentacles.



Figures 131–136. Anatomy of digestive system of *Lusitromina abyssorum* (Lus, 1993). **131–132.** Specimen shown in Figures 107–109, USNM 896525. **131.** Dorsal view of stomach, embedded in digestive gland. **132.** Stomach, opened dorsally along incision shown by dashed line in Figure 131. **133–136.** Specimen shown in Figures 99–100, USNM 1010536. **133.** Left lateral, **134.** ventral, and **135.** right lateral views of anterior alimentary system. **136.** Latero-dorsal view of the anterior oesophagus to show the opening of the duct of gland of Leiblein. Scale bars = 2 mm for Figures 131, 133–135, 1 mm for Figures 132, 136. **a,** anus; **addg,** anterior duct of the digestive gland; **ao,** anterior aorta; **bm,** buccal mass; **dg,** digestive gland; **dgL,** duct of gland of Leiblein; **gL,** gland of Leiblein; **lf,** longitudinal fold; **ls,** lateral sulcus; **lsg,** left salivary gland; **nep,** nephridium; **ng,** nephridial gland; **nr,** circumoesophageal nerve ring; **pddg,** posterior duct of digestive gland; **per,** pericardium; **poe,** posterior oesophagus; **pr,** proboscis; **prr,** proboscis retractors; **rsg,** right salivary gland; **sd,** salivary duct; **ss,** style sac; **st,** stomach; **T1, T2,** major and minor typhlosoles; **vL,** valve of Leiblein.

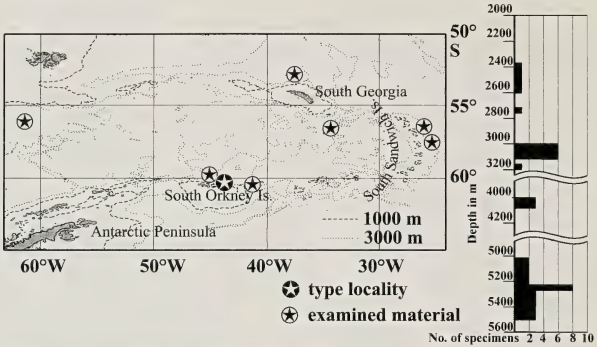


Figure 137. Geographic and bathymetric distribution of *Lusitromina abyssorum* (Lus, 1993).

shaped, without posterior mixing area, with numerous, fine, semicircular dorso-ventral folds. Transition from oesophagus to stomach marked by change from tall longitudinal folds to much finer, curved folds that line stomach. Posterior duct of digestive gland (Figure 132, pddg) large, situated near entrance of oesophagus. Longitudinal fold (Figure 132, lf) narrow, distinct, originates at entrance of oesophagus, runs length of stomach, becomes obsolete near intestine. Anterior duct of digestive gland (Figure 132, addg) small. Lateral sulcus (Figure 132, ls) shallow. Typhlosoles (Figure 132, T1, T2) more prominent in intestine, bordering, deep, narrow intestinal groove. Posterior part of style sac (Figure 132, ss) lined with transverse folds. Folds lining stomach very low, ventral channel of gastric chamber poorly separated from dorsal chamber.

Male Reproductive System: Seminal vesicle of medium size (Figure 127), spans less than ⅓ of whorl, formed of few large loops. Seminal duct descends to floor of mantle cavity at its rear, becomes thickened, sinuous, running to base of penis, where it enters cephalic haemocoel (Figure 125) expands greatly, makes a long loop posteriorly, before entering penis. Penis shorter than mantle cavity, flattened, non-pigmented, with long, cylindrical terminal papilla surrounded by circular fold at its base (Figure 126).

Type Locality: Lorie Trench, off South Orkney Islands, 60°12′9″ S, 43°59′0″ W, in 5450–5480 m. [R/V Akademik Kurchatov, sta. 909, 10 Dec 1971].

Type Material: Holotype and 2 paratypes, from the type locality; 2 paratypes, Orkney Trench, 60°50′5″ S, 41°11′7″ W, in 5063–5470 m, [R/V Dmitriy Mendeleev, sta. 4089, 4 Mar, 1989]. Type material could not be located in the collections of the Institute of Oceanology of Russian Academy of Sciences, Moscow. The type series consists entirely of juvenile specimens. The shell of the holotype (the only intact shell) measured 7.4 mm in length, 5.5 mm in width.

Other Material Examined: SOUTH GEORGIA IS-

Table 5. *Lusitromina abyssorum* (Lus, 1993). Measurements of shell characters. Linear measurements in mm. (n = 5).

Character	Mean	σ	Range
Shell length (SL)	20.9	6.5	12.3–29.2
Final whorl length (FWL)	16.7	4.9	10.3–23.2
Aperture length (AL)	13.4	4.1	8.6–18.9
Siphonal canal length (SCL)	2.5	0.4	1.9–3.3
Shell width (SW)	13.4	4.2	7.9–19.4
FWL/SL	0.80	0.02	0.78–0.84
AL/SL	0.65	0.03	0.61–0.70
SCL/SL	0.12	0.02	0.10–0.16
SW/SL	0.64	0.04	0.60–0.70
Number of spiral cords on penultimate whorl	12.8	6.4	4–20
Number of spiral cords suture to peripheral cord	9.6	7.4	2–20
Number of spiral cords peripheral cord to siphon	35.0	13.1	19–53

LAND: USNM 896525, 53°02′ S, 37°40′ W, in 3056–3102 m. [R/V Eltanin, sta. 735, 13 Sep 1963], 6 specimens (1 adult + 5 juveniles), (anatomy examined); USNM 896533, 56°04′ S, 33°59′ W, in 3138–3239 m, [R/V Eltanin, sta. 722, 8 Sep 1963], 1 specimen. SOUTH SANDWICH ISLANDS: USNM 1010535, E of Candlemas Island, 57°00′24″ S, 26°10′06″ W, in 2740–2757 m. [R/V Islas Orcadas, sta. 38, 22 May 1975], 1 specimen; USNM 1010536, Saunders Island, 57°39′00″ S, 26°00′24″ W, in 2380–2609 m. [R/V Islas Orcadas, sta. 54, 27 May 1975] 1 specimen (radula and anterior foregut anatomy studied). SCOTIA RIDGE: USNM 896800, 56°02′ S, 61°56′ W, in 4008 m. [sta. 112, 20 Jul 1962], 4 specimens (juveniles). SOUTH ORKNEY ISLANDS: USNM 896785, 60°06′ S, 45°26′ W, depth not recorded, but > 5000 m according to the bathymetric Atlas GEBSCO97], [R/V Eltanin, sta. 488, 18 Feb 1963] 1 specimen; USNM 1010537, 60°07′ S, 45°14′ W, 5285 m. [R/V Eltanin, sta. 485, 18 Feb 1963] 8 specimens (juveniles).

Distribution (Figure 137): Within and around the margins of the Scotia Sea, in 2380–5480 m.

Remarks: Lus's (1993) original description of *Tromina abyssorum* is undoubtedly the most extensive of any Antarctic or abyssal buccinoidean in terms of conchological and anatomical detail. She was familiar with Clarke's (1961) work on the abyssal mollusks from the South Atlantic Ocean, and regarded *T. abyssorum* to be closely related to *T. bella abyssicola* Clarke, 1961. She was apparently unfamiliar with Dell's (1990) clarification of the taxonomic affinities of *Tromina,* as discussed in the remarks under *Lusitromina* (above).

DISCUSSION

While exploration of Antarctic Seas began during the second half of the eighteenth century (Conrad, 1999 for chronology), significant additions to our knowledge of their molluscan fauna originated with the cruises of the H.M.S. Challenger (Numanami, 1996: Table 1) and continue to this day. Several of the research cruises during the late 19th and early 20th centuries sampled at least some stations at abyssal depths, yet only a single buccinoidean genus (*Bathydomus* Thiele, 1912) had been described from these depths off Antarctica. Clarke (1961) reported on the abyssal mollusks collected during the cruises of the R/V Vema in the South Atlantic (1957–1958). He recognized five buccinoidean taxa, but attributed them all to the subtidal genus *Tromina.* Following his example, Lus (1993) described a related abyssal to hadal species in the genus *Tromina,* trawled by the Russian vessels R/V Akademik Kurchatov (1971) and R/V Dmitriy Mendeleev (1989) during their explorations of the abyssal benthic faunas of the Weddell and Scotia Seas. The present study, based on material collected by the United States Antarctic Program (USAP) vessels R/V Islas Orcadas, R/V Eltanin and supplemented by samples from the German vessel R/V Polarstern, has increased the number of abyssal buccinoidean genera from the seas surrounding Antarctica to six.

In the course of our study, we have reviewed the taxonomic placement, geographic and bathymetric distribution, diagnostic characters, and diversity of each of the 29 genera that have thus far been proposed for Antarctic and Magellanic Buccinoidea (Appendix 1). The bathymetric ranges of these genera are plotted in Figure 138. We analysed the bathymetric distribution of these taxa by subdividing depth into 200 meter increments, and scoring each genus as present or absent within each increment. Employing the Correlation Distance Measure and Ward's Method for Group Linkage, PC-ORD (McCune and Mifford, 1999) was used to cluster the depth increments based on similarities of their buccinoidean fauna. The resulting dendrogram (Figure 138, Ward's Method) reveals a primary and profound dichotomy in generic composition of the faunas at depths above and below 2200 m, roughly corresponding to the transition from the bathyal to the abyssal zone (Gage and Tyler, 1991). This differentiation of slope and abyssal faunas is absolute, with the two faunas having no genera in common. The apparent minor overlap in the ranges of *Parabuccinum* and *Spikebuccinum* shown in Figure 138 is spurious, as all records for *Parabuccinum* from depths greater than 866 m are based on dead shells (Harasewych, Kantor and Linse, 2000). On a finer scale, the continental shelf (0–200 m; Figure 138: A) and upper continental slope (200–1,000 m; Figure 138: B) faunas are differentiated from the lower slope fauna (1000–2200 m; Figure 138: C), while the abyssal fauna is partitioned into continental rise (2200–3800 m; Figure 138: D), abyssal plain (3800–4800 m; Figure 138: E), and hadal (>4800 m: Figure 138: F) faunas. The pattern of clustering agrees generally with that obtained by Rex (1977: fig. 1) for the deep-sea gastropod fauna of the western North Atlantic, except that, for Antarctic and Magellanic Buccinoidea, the upper continental slope fauna is more similar to the continental shelf fauna than to the lower continental slope fauna.

When assessing the taxonomic placement of genera, we observed that those genera occurring at continental shelf and slope depths conform readily to Powell's (1951) criteria for the subfamilies Buccinulinae, Prosiphiinae and Cominellinae. However, taxa from abyssal and hadal depths do not. It is interesting to note that Powell (1951: 131) had to modify his criteria for Buccinulinae to accommodate *Bathydomus,* the only abyssal genus previously included in his classification. We admit to having similarly modified or expanded subfamilial criteria in order to fit our newly described abyssal taxa into an existing classification for the sake of taxonomic expediency. While the sublittoral and bathyal buccinoideans of Antarctica and the Magellanic Province are likely the product of one, or very few *in situ* evolutionary radiations, the origins and relationships of the abyssal fauna are more complex. For some abyssal genera (e.g., *Spikebuccinum, Germonea, Lusitromina*), credible sister taxa inhabit adjacent continental slopes. For others (e.g., *Dre-*

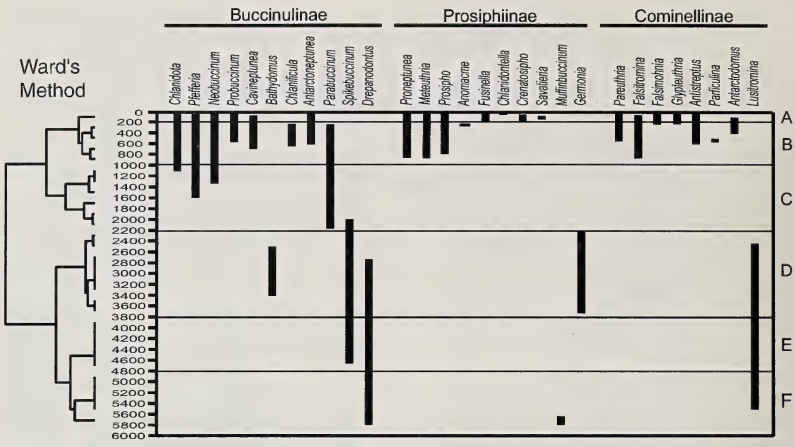


Figure 138. Bathymetric distributions of buccinoidean genera occurring in the Magellanic Province and south of the Antarctic convergence. The dendrogram clusters 200 m increments of depth on the basis of shared buccinoidean genera. A, continental shelf; B, upper continental slope; C, lower continental slope; D, continental rise; E, abyssal plain, F; hadal depths.

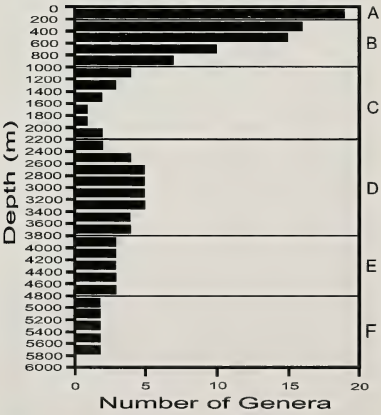


Figure 139. Diversity of buccinoidean genera vs. depth. A, continental shelf; B, upper continental slope; C lower continental slope; D, continental rise; E, abyssal plain; F, hadal depths.

panodontus, Muffinbuccinum), we have noted closer affinities with abyssal or hadal taxa from austral seas beyond the Antarctic convergence. Lipps and Hickman (1982) reviewed various hypotheses regarding origin and age of deep-sea and Antarctic faunas. They concluded that both faunas have evolved primarily in place since at least the Mesozoic, but were supplemented by subsequent minor immigration. Our findings are qualitatively consistant with this hypothesis, indicating that, at least for the Buccinoidea, which have origins in the late Mesozoic, the abyssal Antarctic fauna consists of a combination of taxa, some with nearest relatives, and presumably origins, on the adjacent continental slope, and others with nearest relatives in neighboring ocean basins.

The diversities of both the slope and the abyssal buccinoidean faunas decrease with increasing depth (Figure 139). While the shallower components of each fauna tend to have narrow bathymetric ranges and the deeper dwelling genera tend to have broader bathymetric ranges, most genera span two or three bathymetric regions. Only 4 of 19 sublittoral genera (21.1%) are confined to the continental shelf, while 3 of 16 (18.8%) upper slope genera and 0 of 4 lower slope genera (0%) are limited to a single region. Within the abyssal zone, 2 of 5 genera (40.0%) are known only from the continental rise, while none of the 3 genera that occur on the abyssal plain are restricted to it. Of the 3 hadal genera, only one (33.3%), *Muffinbuccinum*, is restricted to this zone. The genus *Muffinbuccinum* is presently known from a single sta-

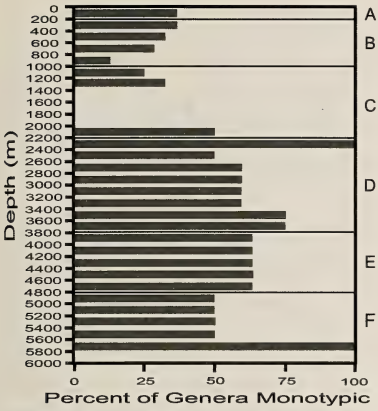


Figure 140. Proportion of monotypic genera vs. depth. A, continental shelf; B, upper continental slope; C, lower continental slope; D, continental rise; E, abyssal plain; F, hadal depths.

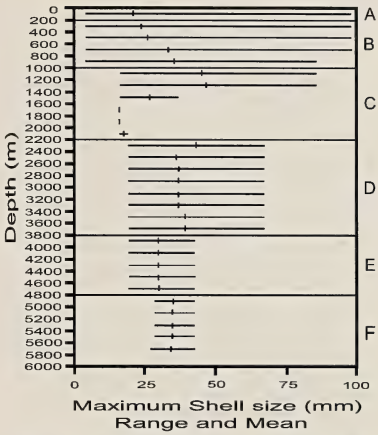


Figure 141. The range and mean of maximum shell size within a genus vs. depth. A, continental shelf; B, upper continental slope; C, lower continental slope; D, continental rise; E, abyssal plain; F, hadal depths.

tion. *Drepanodontus,* which co-occurs with *Muffinbuccinum* at this station, has a much broader bathymetric range. For the abyssal buccinoideans, the maximum generic diversity occurs from 2600 to 3200 m, which closely corresponds to the depths for peak of gastropod species richness reported by Rex (1981: fig. 1).

The buccinoidean fauna of the Antarctic and Magellanic Provinces contains an extraordinarily high proportion (14 out of 29, 48.3%) of genera known only from their type species. In comparison, of 33 genera of boreal Buccinidae, only 5 (15.2%) are monotypic. When plotted by depth (Figure 140), it is evident that the abyssal fauna has a much higher fraction of such genera. The bathymetric distribution of monotypic genera at abyssal depths in the Southern Ocean appears to be the inverse of that predicted by a plot of species per genus ratios against depth (Rex, 1983: fig. 4). Based on samples from the NW Atlantic Ocean, the number of species per genus actually peaks between 2000 and 3000 m. Data are insufficient to determine if this pattern represents a real biological phenomenon (true monotypy as the result of an early adaptive radiation into the deep-sea around Antarctica without subsequent diversification), or is an artefact of low sampling density exacerbated by difficulties in differentiating closely related species. As noted by Gage and Tyler (1991: 204), the few large data sets that are available for deep-sea faunas have produced rarefaction curves that do not even approach their asymptote, the point at which additional sampling will no longer discover new taxa. While buccinoidean genera have historically been based on features of the shell, operculum and radula, species within genera tend to have very similar opercula and radulae, and are usually differentiated primarily on shell morphology. Increases in latitude and depth each contribute to a reduction in the amount of calcium carbonate in seawater, which, in turn, has profound effects on shell thickness, geometry and the presence of sculpture (Graus, 1974). High latitude and deep-water gastropods often have shells that are thin, roughly spherical (minimizing the ratio of surface area to volume), and lack pronounced surface sculpture. There are numerous examples in the Antarctic fauna of such convergent ecophenotypic similarities in shell form obscuring phylogenetic relationships, even at the level of families and superfamilies (e.g., discussions of *Tromina* and *Notoficula* in Appendix 1; Kantor and Harasewych, 1999, 2000). Some of the genera now regarded as monotypic will likely be discovered to contain additional cryptic or sibling species with similar shell and/or radular morphologies when investigated using molecular or multivariate morphometric techniques.

A number of authors (e.g., Lipps and Hickman, 1982; Gage and Tyler, 1999) have noted the prevalence of both gigantism and small body size in organisms from the Antarctic and the deep-sea. Rex et al. (1999) reported that size increases significantly with depth from upper bathyal region to the abyssal plain for the related neogastropod family Turridae. They suggested that larger size may be favored at greater depths because of its met-

abolic and competitive advantages, and noted that the density of polychaete worms, a major food source for Turridae as well as buccinoideans (Taylor, 1978), decreases exponentially with depth.

We plotted the range and mean of maximum shell sizes of all genera occurring within each 200 m bathymetric increment (Figure 141). The continental shelf and upper continental slope support the largest as well as the smallest buccinoidean genera, with the range in size narrowing as depth increases. The mean of the maximum sizes of genera increases from the continental shelf to the lower slope, before decreasing abruptly at the base of the continental slope. The trend of decreasing size range with increasing depth is repeated in the abyssal fauna, with the largest genera and the broadest range in size occurring along the continental rise. Despite the differences in taxa, ocean basins, and sample sizes between the work of Rex et al. (1999: fig. 2) and the present study, both indicate that taxa inhabiting the base of the continental slope are smaller than those of either the upper slope or continental rise, and that maximum shell size is reached near the boundary of the continental rise and abyssal plain, and subsequently decreases with increasing depth.

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Appendix 1. A review of the taxonomic placement of the genera of Antarctic and Magellanic Buccinulidae.

The family Buccinulidae was proposed by Finlay (1928: 250) to unite a number of genera from the region of New Zealand that had previously been included in Muricidae, Neptuniidae (as Chrysodomidae), and Buccinidae by earlier workers (Hutton, 1880; Cossmann, 1906; Suter, 1913). Shortly thereafter, Powell (1929: 58) expanded and revised Finlay's classification based mainly on the morphology of the radula, sorting primarily austral genera into the families:

Buccinulidae. Recognized by having a radula with 3 cusps on rachidian teeth and 3 cusps on lateral teeth, and an operculum with a terminal nucleus. This family was further subdivided into groups A–E based on morphology of the siphonal canal, parietal tubercle, and protoconch.

Neptuniidae. Recognized by having a radula with 4 cusps on rachidian teeth and 3 cusps on lateral teeth. The operculum also has a terminal nucleus.

Buccinidae. Characterized by having a radula with about 6 cusps on rachidian teeth and 4 cusps on lateral teeth. The operculum has a median, submarginal nucleus.

Cominellidae. Distinguished by having a radula with 3 cusps on rachidian teeth, 2 cusps on lateral teeth, and an operculum with a terminal nucleus.

Published the same year, Thiele's (1929) treatment of the Stenoglossa interpreted the family Buccinidae far more broadly, subsuming all of the families treated by Powell (1929) without recognizing any natural groupings or subdivisions. Powell (1951: 131) proposed a revised classification of the southern whelks, reaffirming his earlier (Powell, 1929) narrower interpretation of Buccinidae (limited to the genera *Buccinum* Linné, 1758 and *Burnupena* Iredale, 1918), and stating that the Buccinulidae were more closely related to the northern Neptuniidae than to the Buccinidae. He subdivided the Buccinulidae into the subfamilies Buccinulinae, Prosiphiinae and Cominellinae. In subsequent works, Powell (1960) again elevated Cominellinae to family status. In the section below, we list chronologically the genera originally assigned to each subfamily by Powell (1951), update the systematics for Antarctic and Magellanic genera, and add genera from this region that were published subsequently.

Family Buccinulidae Finlay, 1928

Subfamily Buccinulinae Finlay, 1928.
Defined on the basis of a radula with three cusps on the rachidian teeth and three cusps on the lateral teeth. Originally included genera:

New Zealand: *Buccinulum* Swainson, 1837; *Aeneator* Finlay, 1926; *Verconella* Iredale, 1915.
Australia: *Austrosipho* Cossmann, 1906; *Berylsma* Iredale, 1924.
California: *Kelletia* Bayle, 1884.

Antarctic and Subantarctic: *Chlanidota* Martens, 1878; *Pfefferia* Strebel, 1908 (reduced to a subgenus of *Chlanidota* by Harasewych and Kantor, 1999); *Neobuccinum* Smith, 1877; *Probuccinum* Thiele, 1912; *Cavineptunea* Powell, 1951; *Bathydomus* Thiele, 1912. [additional genera: *Chlanificula* Powell, 1958; *Antarctoneptunea* Dell, 1972; *Parabuccinum* Harasewych, Kantor and Linse, 2000; *Spikebuccinum* Harasewych and Kantor, herein; *Drepanodontus* Harasewych and Kantor, herein].

Neobuccinum Smith, 1877

Type Species: *Buccinopsis eatoni* Smith, 1875 (by monotypy).
Distribution: Circum-Antarctic, Kerguelen and Heard Islands, in 6–1335 m.
Remarks: Shell large (to 86 mm). Operculum large, occupying nearly entire aperture, oval, paucispiral. Rachidian teeth with 3 strong cusps, broad basal plate. Lateral teeth with 3 cusps, middle cusp small.
Diversity: Currently a monotypic genus. Numanami (1996: 147) noted some geographical differences in shell morphometry.

Chlanidota (*Chlanidota*) Martens, 1878

Type Species: *Cominella* (*Chlanidota*) *vestita* Martens, 1878 (by monotypy).
Distribution: Circum-Antarctic. Kerguelen Island, the Crouzets, Herald Island, South Georgia Island, Antarctica, in 3–1100 m.
Remarks: Shell medium-sized (to 43 mm). Operculum very small (less than 0.4 AL), coiled, with terminal nucleus. Rachidian teeth with 3 strong cusps, broad, anteriorly indented basal plate, lateral teeth with 3 cusps, middle cusp small.
Diversity: 5 species (recent revision—Harasewych and Kantor, 1999).

Chlanidota (*Pfefferia*) Strebel, 1908

Type species: *Pfefferia palliata* Strebel, 1908 (by subsequent designation, Wenz, 1943).
Distribution: South Georgia Island, in 45–1600 m.
Remarks: Shell medium-sized (to 38 mm). Operculum large (0.5–0.8 AL), leaf-shaped, coiled, with terminal nucleus. Posterior edge of operculum with tall ridge of feathered lamellae. Rachidian teeth with 3 strong cusps, broad, anteriorly indented basal plate. Lateral teeth with 3 cusps, middle cusp small.
Diversity: 3 species (recent revision—Harasewych and Kantor, 1999).

Probuccinum Thiele, 1912

Type species: *Neobuccinum tenerum* Smith, 1907 (by subsequent designation, Wenz, 1943).

Distribution: Circum-Antarctic, in 50–590 m.
Remarks: Shell medium-sized (to 30 mm). Operculum large (~⅔ AL), with terminal nucleus. Rachidian teeth with 3 cusps, central cusp largest, may bear denticles (Numanami, 1996: fig. 104H); basal plate broad, rectangular. Lateral teeth with 3 cusps of approximately equal size.
Diversity: 8 species (Powell, 1960).

Bathydomus Thiele, 1912

Type species: *Bathydomus obtectus* Thiele, 1912 (by original designation).
Distribution: Antarctic, Marion Island and Crozets, in 2500–3400 m.
Remarks: Shell medium-sized (to 30 mm). Operculum large (~0.5 AL) long, narrow, wedge-shaped, with terminal nucleus. Rachidian teeth with 3 strong cusps, middle cusp largest, flanked by 1 weak denticles on each side. Basal plate broad, squarish, anteriorly indented. Lateral teeth with 2 large cusps with 2–3 smaller cusps between them (Thiele, 1912: pl. 16, fig. 23).
Diversity: 3 species (Dell, 1990: 198).

Cavineptunea Powell, 1951

Type species: *Cavineptunea monstrosa* Powell, 1951 (by original designation).
Distribution: South Georgia Island, in 90–700 m.
Remarks: Shell large (to 70 mm), with characteristic protoconch, "like a tall, spirally wound collar, and surrounds a deep apical cavity" (Powell, 1951: fig. N105). Operculum large (~⅔ AL), with terminal nucleus. Rachidian teeth with 3 cusps, central cusp largest, broad, anteriorly indented basal plate. Lateral teeth usually with 3, occasionally 4 cusps, outermost cusps largest.
Diversity: A monotypic genus.

Chlanificula Powell, 1958

Type species: *Chlanificula thielei* Powell, 1958 (by original designation).
Distribution: Weddell Sea to off Enderby Land, Antarctica, in 220–660 m.
Remarks: Shell medium-sized (to 30 mm). Operculum large, occupying nearly entire aperture, narrow, wedge-shaped, with terminal nucleus. Rachidian teeth with strong central cusp, flanked by one smaller cusp and one denticle on each side. Basal plate squarish, shallowly indented anteriorly. Lateral teeth with 3 cusps, middle cusp smaller, additional denticles may appear between cusps (Hain, 1990: pl. 23, fig. 2). Powell (1958) regarded this genus to be part of the "*Chlanidota* complex" closest to *Notoficula*. The genus *Notoficula* Thiele, 1917, has been transferred to Eratoidae by Oliver (1983) based on radular morphology.
Diversity: A monotypic genus.

Antarctoneptunea Dell, 1972

Type species: *Fusitriton aurora* Hedley, 1916 (by original designation).
Distribution: Ross Sea to off Enderby Land, Antarctica, 15–603 m.
Remarks: Shell large (to 102 mm). Operculum large (~⅔ AL), with terminal nucleus. Rachidian teeth with three cusps. Basal plate broad, deeply indented anteriorly. Lateral teeth with 3 cusps, middle cusp smaller. This genus is hardly distinguishable from *Penion* Fischer, 1884 in general shell shape, radula and operculum (Ponder, 1973).
Diversity: A monotypic genus.

Parabuccinum Harasewych, Kantor and Linse, 2000

Type species: *Chlanidota bisculpta* Dell, 1990 (by original designation).
Distribution: Magellanic region, in 247–2165 m.
Remarks: Shell small (to 16.5 mm). Operculum large (> 0.5 AL), oval, paucispiral. Rachidian teeth with 3 strong cusps, broad, anteriorly indented basal plate. Lateral teeth with 3 cusps, middle cusp small. Included in Buccinulinae by Harasewych, Kantor and Linse (2000).
Diversity: 4 species (recent revision—Harasewych, Kantor and Linse, 2000).

Spikebuccinum Harasewych and Kantor, herein.

Type species: *Spikebuccinum stephaniae* Harasewych and Kantor, herein (by original designation).
Distribution: Scotia Sea and adjacent abyssal plains, in 1967–4643 m.
Remarks: Shell small (to 19.9 mm). Operculum small (~0.36 AL), broadly ovate, paucispiral, with subterminal nucleus. Rachidian teeth with 3 cusps, central shorter, weaker that outer cusps. Basal plate broad, deeply indented. Lateral teeth with large outer, smaller inner cusp, with 3–4 smaller denticles between them.
Diversity: A monotypic genus.

Drepanodontus Harasewych and Kantor, herein.

Type species: *Drepanodontus tatyanae* Harasewych and Kantor, herein (by original designation).
Distribution: Scotia Sea and adjacent Argentine Abyssal Plain, in 2740–5798 m.
Remarks: Shell large (to 43.1 mm). Operculum large (~0.82 AL), oval, with terminal nucleus. Rachidian teeth usually with 3 cusps, central cusp large, may or may not be flanked by one lateral cusp and additional denticles. Basal plate narrow, rectangular, weakly indented. Lateral teeth with 1 cusp, which may bear 1 or more denticles, near inner edge of basal plate.
Diversity: A monotypic genus.

Subfamily Prosiphiinae Powell, 1951

Defined on the basis of a radula with 3 cusps on the rachidian teeth, and lateral teeth with multiple cusps.

Contains taxa with heterogeneous lateral tooth morphologies, that may be divided into: *Proneptunea* type lateral teeth, with multiple cusps spanning the width of the basal plate, usually fused above the basal plate, may have one or more denticles along the outer edge; *Prosipho* type lateral teeth, with cusps confined to inner portion of basal plate, often rotated to form an acute angle with the basal plate, the outer portion of which is thin and lacks teeth. Prosiphiinae appear to be restricted to Antarctic and subantarctic seas. Originally included genera:

Antarctic and subantarctic: *Proneptunea* Thiele, 1912; *Meteuthria* Thiele, 1912; *Prosipho* Thiele, 1912; *Anomacme* Strebel, 1905; *Fusinella* Thiele, 1917 (replacement name for *Buccinella* Thiele, 1912, non Perry, 1811); *Chlanidotella* Thiele, 1929. [additional genera: *Savatieria* Rochebrune and Mabille, 1885; *Crenatosipho* Linse, 2002; *Muffinbuccinum* Harasewych and Kantor, herein; *Germonea* Harasewych and Kantor, herein].

Savatieria Rochebrune and Mabille, 1885

Type species: *Savatieria frigida* Rochebrune and Mabille, 1885 (by monotypy).
Distribution: Magellanic region, in 100 m.
Remarks: Shell small (usually < 10 mm). Operculum large, oval, with terminal nucleus. Radula *Prosipho* type. Rachidian teeth narrow, with 3 cusps. Lateral teeth with 4 short, broad cusps, basal plate prolonged anteriorly.
Diversity: 7 species (Powell, 1960: 149).

Anomacme Strebel, 1905

Type species: *Anomacme smithi* Strebel, 1905 (by monotypy).
Distribution: Magellanic region, 220–250 m.
Remarks: Shell small (< 10 mm). Operculum not described. Radula *Prosipho* type. Rachidian teeth with 3 cusps, basal plate squarish, broader than long, weakly indented anteriorly. Lateral teeth with long, narrow basal plate, with 6 cusps concentrated toward the inner portion of the radular tooth, 4th cusp longest (Thiele, 1912: pl. 16, fig. 14). This genus was included in Cominellidae by Powell (1960: 149), presumably because of its similarity in shell shape to *Glypteuthria,* despite its different radular morphology.
Diversity: A monotypic genus.

Proneptunea Thiele, 1912

Type species: *Proneptunea amabilis* Thiele, 1912 (by original designation).
Distribution: Kerguelen, South Georgia Island, South Orkney Islands, Ross Sea, Antarctica, in 12–870 m.
Remarks: Shell small (< 15 mm). Operculum medium-sized, oval, with terminal nucleus. Radula *Proneptunea* type. Rachidian teeth with 3 cusps. Basal plate longer than wide, shallowly indented anteriorly. Lateral teeth broad, spatulate, with 5 long cusps fused above basal plate. Outer edge may have multiple denticles (Powell, 1951: fig. K 66–67).
Diversity: 5 species (Dell, 1990: 199).

Meteuthria Thiele, 1912

Type species: *Euthria martensi* Strebel, 1905 (by original designation).
Distribution: Magellanic region, and Ross Sea, Antarctica, in 57–870 m.
Remarks: Shell very small (< 5 mm). Operculum undescribed. Radula *Prosipho* type, without rachidian teeth. Lateral teeth with multiple (4–5) cusps concentrated toward inner portion of tooth. Outermost cusp may have denticles (Powell, 1951: fig. K62; Dell, 1990: fig. 296). This genus was included in the subfamily Cominellidae by Powell (1960: 149), presumably because of its similarity in shell shape to *Glypteuthria,* despite its different radular morphology.
Diversity: 4 species, 1 subspecies (Powell, 1960: 149; Dell, 1990: 173).

Prosipho Thiele, 1912

Type species: *Prosipho gaussianus* Thiele, 1912 (by subsequent designation, Thiele, 1929).
Distribution: Circum-Antarctic, in 12–800 m.
Remarks: Shell small, rarely > 10 mm. Operculum large (~⅔ AL), oval, with coiled nucleus. Radula *Prosipho* type. Rachidian teeth with 3 cusps, basal plate squarish to longer than broad, weakly indented anteriorly. Lateral teeth with long, narrow basal plate, with 2 or more cusps concentrated toward the inner portion of the radular tooth.
Diversity: About 40 species (Powell, 1951; Dell, 1990; Numanami, 1996).

Fusinella Thiele, 1917 (replacement name for *Buccinella* Thiele, 1912, non Perry, 1811)

Type species: *Buccinella jucunda* Thiele, 1912 (by monotypy).
Distribution: Kerguelen Island, 0–100 m.
Remarks: Shell very small (< 6 mm). Operculum oval, with terminal nucleus. Radula *Prosipho* type. Rachidian teeth with 3 cusps of equal size near center, with an additional cusp at each posterior corner of the squarish basal plate with a deep, V-shaped indentation anteriorly. Lateral teeth with long, narrow basal plate, with multiple (5–6) cusps concentrated along inner half of basal plate and directed parallel to its long axis (Thiele, 1912: pl. 16, fig. 13).
Diversity: A monotypic genus.

Chlanidotella Thiele, 1929

Type species: *Cominella modesta* Martens, 1885 (by monotypy).

Distribution: South Georgia, 0–18 m.
Remarks: Shell medium-sized (< 15 mm). Operculum medium-sized (~0.5 AL), oval, with terminal nucleus. Radula *Proneptunea* type. Rachidian teeth with 3 cusps, central cusp slightly longer than flanking cusps. Basal plate broader than long, deeply indented anteriorly. Lateral teeth with 4 cusps roughly equal in length, spanning the entire width of the basal plate. Thiele's illustration (1912: textfig. 11) of the radula shows a denticle along the outer edge along one side of the radula, while Powell's illustration (1951: fig. L 80) does not.
Diversity: A monotypic genus.

Crenatosipho Linse, 2002

Type species: *Crenatosipho beaglensis* Linse, 2002 (by original designation).
Distribution: Magellanic region, in 67–200 m.
Remarks: Shell small (to 9 mm). Operculum large, oval with eccentric nucleus. Radula *Prosipho* type. Rachidian teeth very narrow, long, without cusps. Lateral teeth with up to 6 cusps long concentrated toward the inner margin of the tooth, with long, cuspless outer portion of the basal plate. (Linse, 2002: fig. 9.1.1–112).
Diversity: A monotypic genus.

Muffinbuccinum Harasewych and Kantor, herein

Type species: *Muffinbuccinum catherinae* Harasewych and Kantor, herein (by original designation).
Distribution: Argentine Abyssal Plain, off the northern slope of the Falkland Plateau, in 5685–5798 m.
Remarks: Shell of moderate size (to 27 mm). Operculum large (~0.56 AL), triangular, tapering toward terminal nucleus. Radula *Proneptunea* type. Rachidian teeth with 3 cusps, central cusp slightly longer than flanking cusps. Basal plate broad, short, shallowly indented anteriorly. Lateral teeth with 7–8 cusps spanning basal plate, innermost cusp longest, outermost shortest, with or without denticles along outer edge.
Diversity: A monotypic genus.

Germonea Harasewych and Kantor, herein

Type species: *Germonea rachelae* Harasewych and Kantor, herein (by original designation).
Distribution: Abyssal plain of the Scotia Sea, in 2196–3714 m.
Remarks: Shell large (to 68 mm). Operculum large (~0.65 AL), narrow, recurved, with terminal nucleus. Radula *Prosipho* type. Rachidian teeth with 3 cusps, very long, narrow, deeply indented anteriorly, appearing Y-shaped. Lateral teeth with 3–4 broad, stout cusps concentrated toward the inner margin of the tooth, with short, cuspless outer portion of the basal plate.
Diversity: A monotypic genus.

Subfamily Cominellinae Gray, 1857

Defined on the basis of a radula with 3 cusps on the rachidian tooth, and lateral teeth with 2 cusps. Originally included genera:
New Zealand and Australia: *Cominella* Gray, 1850; *Fax* Iredale, 1925.
Tropical Pacific: *Phos* Montfort, 1810.
Northwest Pacific: *Searlesia* Harmer, 1914.
Antarctic and Subantarctic: *Pareuthria* Strebel, 1905; *Tromina* Dall, 1918; *Notoficula* Thiele, 1917 [now in Eratoidae]; *Falsimohnia* Powell, 1951; *Glypteuthria* Strebel, 1905. [additional genera: *Antistreptus* Dall, 1902; *Parficulina* Powell, 1958; *Antarctodomus* Dell, 1972; *Lusitromina* Harasewych and Kantor, herein].

Antistreptus Dall, 1902

Type species: *Antistreptus magellanicus* Dall, 1902 (by original designation).
Distribution: Magellanic region, in 30–600 m.
Remarks: Shell very small (< 5 mm), sinistral. Operculum described but not figured by Linse (2002: 100) as "small, horny, brown, thin, eccentric, with a large oval foot muscle scar." The radula is unknown. Apart from being sinistral, shell shape is similar to *Glypteuthria* and *Anomacme*. This genus was described within Muricidae and compared to *Trophon* by Dall (1902). Powell (1951) included it in Buccinulidae, but later placed it in Cominellidae (Powell, 1960).
Diversity: 2 species, *Antistreptus magellanicus* Dall, 1902, *A. rolani* Castellanos, 1985.

Pareuthria Strebel, 1905

Type species: *Fusus plumbeus* Philippi, 1844 (by subsequent designation, Tomlin, 1932).
Distribution: Magellanic region, Circum-Antarctic, in 0–549 m.
Remarks: Shell small (< 10 mm). Operculum ovate, with terminal nucleus. Despite shell similarities between Magellanic and Antarctic species, there are conspicuous differences in radular dentition between species inhabiting these regions. Magellanic species, including the type species of the genus, have broad rachidian teeth with 3 subequal cusps. Antarctic species have rachidian teeth with squarish basal plates and a large triangular central cusp that may or may not be flanked by one or rarely more (Numanami, 1996: fig. 125D), smaller denticles on each side. Lateral teeth with long, stout basal plates that give rise to 2 long, recurved cusps.
Diversity: About 18 species (Powell, 1960; Numanami, 1996).

Glypteuthria Strebel, 1905

Type species: *Euthria meridionalis* Smith, 1881 (by subsequent designation, Tomlin, 1932).

Distribution: Magellanic region, Southern Africa, in 6–250 m.
Remarks: Shell medium-sized (< 29 mm). Operculum ovate, with terminal nucleus. Rachidian teeth with 3 cusps on squarish, posteriorly indented basal plate. Lateral teeth with broad basal plate, 3 cusps, inner and outer cusps long, intermediate cusp short. Powell (1951: 138) regarded *Glypteuthria* to be a strongly sculptured relative of *Pareuthria,* with the intermediate cusp a bifurcation of the inner cusp, and not comparable to the 3rd cusp of *Probuccinum.*
Diversity: 7 species, 4 Magellanic, 3 South African.

Notoficula Thiele, 1917 (New name for *Ficulina* Thiele, 1912, *non* Gray, 1867)

Type species: *Ficulina bouveti* Theile, 1912 (by monotypy). The anatomy, radular morphology, and operculum of the type species remain unknown. Oliver (1983) described an additional species of *Notoficula,* and, based on its radular morphology and anatomy, transferred the genus to Eratoidae. Powell (1958: 192) reconsidered the affinities of the species he originally described as *Notoficula problematica* Powell, 1951, and erected the genus *Parficulina* Powell, 1958 to accommodate it (see below).

Tromina Dall, 1918

Type species: *Fusus unicarinatus* Philippi, 1868 (by original designation). The type species of this genus was shown to belong to the family Muricidae. Dell (1990) proposed the name *Falsitromina* to include the bathyal Magellanic buccinoidean taxa previously included in *Tromina.* The genus *Lusitromina* is proposed herein for the abyssal species that had been assigned to *Tromina.* For a detailed review of the taxonomy of *Tromina,* see the "Remarks" section under the description of *Lusitromina.*

Falsimohnia Powell, 1951

Type species: *Buccinum albozonatum* Watson, 1881 (by original designation).
Distribution: South Georgia, Kerguelen Island, in 18–250 m.
Remarks: Shell small (< 10 mm), operculum small, with blunt, terminal nucleus. Rachidian tooth with single, triangular cusp on squarish basal plate with shallow anterior indentation. Lateral teeth with long basal plate giving rise to 2 teeth, outermost broader, longer. Powell (1951: 137) regarded *Falsimohnia* to be derived from *Pareuthria.*
Diversity: A monotypic genus (see comments under *Antarctodomus* diversity).

Parficulina Powell, 1958

Type species: *Notoficula problematica* Powell, 1951 (by original designation).
Distribution: Magellanic region, in 545 m.
Remarks: Shell small (to 7 mm). Operculum medium sized (~0.50 AL), D-shaped, paucispiral. Rachidian teeth with 3 equal cusps on a squarish basal plate. Lateral teeth with 2 cusps, the inner cusp much broader than the outer cusp. See remarks under *Notoficula* (above).
Diversity: A monotypic genus.

Antarctodomus Dell, 1972

Type species: *Bathydomus thielei* Powell, 1958 (by original designation).
Distribution: Eastern hemisphere, from the Ross Sea to off Queen Maud Land, Antarctica, 110–420 m.
Remarks: Shell medium-sized (to 30 mm). Operculum long, triangular, with terminal nucleus (Dell, 1972). Rachidian tooth with 3 cusps, basal plate broad, short, deeply indented anteriorly. Lateral teeth with 2 long, blunt, cusps, basal plate narrower than rachidian teeth.
Diversity: 2 species (Numanami, 1996: 147. In our view, *Antarctodomus okutanii* Numanami, 1996 differs in opercular and radular morphology from the type species of *Antarctodomus,* and may be referable to *Falsimohnia*).

Falsitromina Dell, 1990

Type species: *Tromina bella* Powell, 1951 (by original designation).
Distribution: Magellanic region, in 81–878 m [Dell (1990: 175) reported but did not illustrate or provide catalog numbers for two specimens he attributed to *F. bella* from the Ross Sea, at depths of 1565–1674 m.]
Remarks: Shell small (to 14 mm). Operculum medium-sized (~0.50 AL), oval, paucispiral. Rachidian teeth with 3 cusps, central cusp may be slightly longer, on a squarish basal plate, shallowly indented anteriorly. Lateral teeth with two broad curved cusps that join above the basal plate.
Diversity: 5 species (Dell, 1990).

Lusitromina Harasewych and Kantor, herein

Type species: *Tromina abyssorum* Lus, 1993 (by original designation).
Distribution: Scotia Sea, and adjacent abyssal plains, Cape Basin, in 2380–5480 m.
Remarks: Shell medium sized (to 29 mm). Operculum D-shaped, large (~0.61 AL), broadly ovate, paucispiral. Rachidian teeth with 3 cusps on posterior portion of broad, anteriorly arched basal plate. Central cusp slightly longer, wider than lateral cusps. Lateral teeth with 2 cusps of approximately equal length.
Diversity: 2 species.

New species of Late Cretaceous Cypraeidae (Gastropoda) from California and British Columbia and new records from the Pacific slope

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ABSTRACT

Cretaceous cypraeids are uncommon in North American strata and comprise 15 recognized species, seven of which are from the Pacific slope of North America (Groves, 1990). Four new species are described herein from localities in southern and northern California and British Columbia, Canada: *Palaeocypraea* (*Palaeocypraea*) *wilfredi* new species and *Bernaya* (*Bernaya*) *jeanae* new species, both from the Upper Cretaceous (lower Campanian) Chico Formation, Butte County, California; *Bernaya* (*Bernaya*) *beardi* new species from the Upper Cretaceous (uppermost Santonian to lowermost Campanian) upper Haslam Formation, Vancouver Island, British Columbia, Canada; and *Bernaya* (*Protocypraea*) *popenoei* new species from the Upper Cretaceous (lower Campanian) Ladd Formation, Orange County, California. The late Campanian to early Maastrichtian was the Mesozoic peak of cypraeids, in terms of numbers of species and geographic distribution both in North America and worldwide (Groves, 1994). New paleogeographic and chronologic records of previously described species and indeterminate species are listed as well.

INTRODUCTION

Four new Late Cretaceous species of cypraeid gastropods, uncommon in strata of that geologic age in North America, are described from localities in Orange and Butte counties, California, and Vancouver Island, British Columbia (Figure 1). Two are from the lower Campanian Chico Formation, Butte County, California; the third is from the uppermost Santonian to lowermost Campanian upper Haslam Formation, near Brannen Lake, Vancouver Island, British Columbia, Canada; and the fourth new species is from the lower Campanian Holz Shale Member of the Ladd Formation, Santa Ana Mountains, Orange County, California. Cypraeid records from the Chico and Ladd formations are recorded here for the first time.

STRATIGRAPHY AND GEOLOGIC AGE

The formations listed below, from oldest to youngest, are those from which the new cypraeid taxa are described. Squires and Saul (2001) recently described several new species of gastropods from these formations and discussed their geologic age, stratigraphy, and paleoenvironment. Therefore, only a brief overview of stratigraphic nomenclature and age of the units will be discussed and readers are referred to additional sources for detailed descriptions.

Haslam Formation

The Haslam Formation of Clapp (1912) was described for outcrops on southeastern Vancouver Island, British Columbia. Based on ammonite biostratigraphy, Muller and Jeletzky (1970) cited the age of the formation as late Santonian to early Campanian, as did Ward (1978) and Haggart (1991). Squires and Saul (2001) concurred with a late Santonian to early Campanian age for the formation and indicated that magnetostratigraphic analysis could more precisely refine the stage boundary. Magnetostratigraphic work by Enkin et al. (2001 and pers. commun.) indicated that the formation was entirely Campanian. However, most recently Mustard et al. (2003 and pers. commun.) concluded that the formation was diachronous and contained both late Santonian and early Campanian fossils.

Pentz Road member of the Chico Formation

Russell et al. (1986) described the informal Pentz Road member of the Chico Formation for outcrops near "Pence's Ranch" (= Pentz), Butte County, northern California. Based on the presence of the ammonites *Submortoniceras chicoense* (Trask, 1856) and *Baculites chicoensis* (Trask, 1856), they assigned an early Campanian age to these outcrops. Interestingly, Haggart et al. (1997)

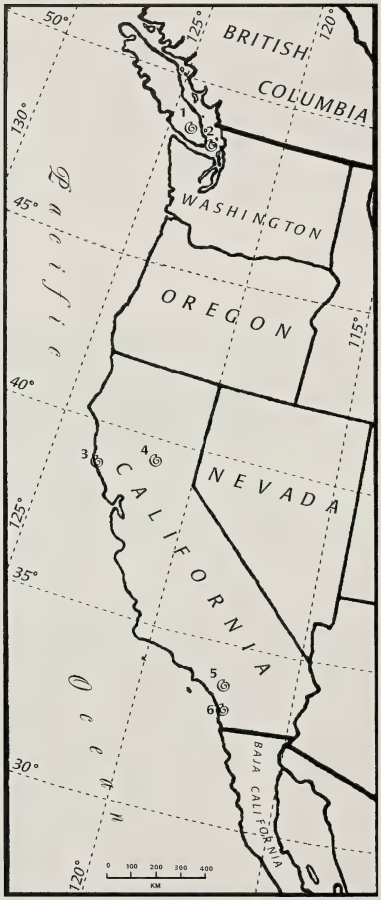


Figure 1. Index map showing type localities for new taxa and other pertinent geographic areas mentioned in the text (modified with permission from Squires and Saul, 2001). 1 = Vancouver Island, British Columbia; 2 = Sucia Island, San Juan County, Washington; 3 = Gualala, Mendocino County, California; 4 = Pentz, Butte County, California; 5 = Santa Ana Mountains, Orange County, California; 6 = Carlsbad, San Diego County, California.

informally named a Pentz member for the same beds described by Russell et al. (1986) and interpreted these facies as a very nearshore shallow-marine environment. Squires and Saul (1997; 2001) concurred with the early Campanian age; based on the presence of the soft-bottom dwelling gastropod *Boggsia tenuis* (Gabb, 1864), however, they also interpreted the paleoenvironment as shallow marine rather than the estuarine environment reported by Russell et al. (1986).

Holz Shale Member of the Ladd Formation

Popenoe (1942) described the Holz Shale Member of the Ladd Formation for lower Campanian outcrops in Ladd Canyon, Santa Ana Mountains, Orange County, California. The fossiliferous upper part of the member is dominated by sandstone beds deposited in a deep-shelf environment (Squires and Saul, 2001).

ABBREVIATIONS

Abbreviations used for institutional catalog and/or locality numbers are as follows: CAS, California Academy of Sciences, San Francisco; CIT, California Institute of Technology (collections now at LACMIP); LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; RBCM, Royal British Columbia Museum, Vancouver; SC, Sierra College, Rocklin, California; SDSNH, San Diego Society of Natural History; UCLA, University of California, Los Angeles (collections now at LACMIP); UCMP, University of California, Museum of Paleontology, Berkeley; USGS, United States Geological Survey, Menlo Park, California (collections now at UCMP); and VIPM, Vancouver Island Paleontological Museum, Qualicum Beach, Vancouver Island, British Columbia, Canada. Measurement parameters are defined as follows: length = greatest distance between anterior and posterior ends; width = greatest distance between lateral margins; and height = greatest distance between base and dorsum. The systematic classification herein follows that of Schilder and Schilder (1971).

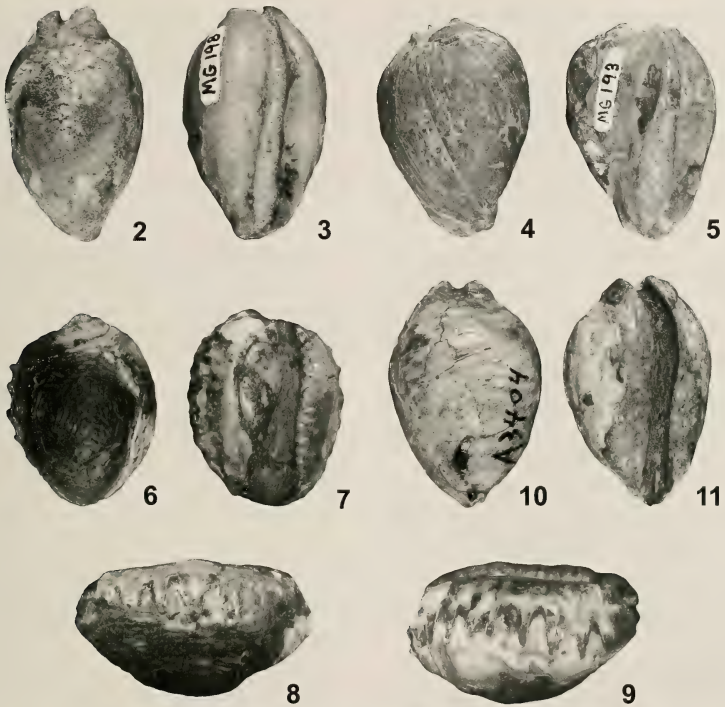
SYSTEMATIC PALEONTOLOGY

Superfamily Cypraeoidea Rafinesque, 1815
Family Cypraeidae Rafinesque, 1815
Subfamily Bernayinae Schilder, 1927
Tribe Archicypraeini Schilder, 1927
Genus *Palaeocypraea* Schilder, 1928

Type Species: *Cypraeacites spiratus* Schlotheim, 1820 by original designation. Early Paleocene (Danian), Faxe, Denmark.

Diagnosis: Shell small to medium in size, elongated, spire broad and partially covered, aperture wide with deep terminal canals and fine dentition; fossula broad, concave and smooth.

Remarks: Schilder and Schilder (1971) recognized



Figures 2, 3. *Palaeocypraea* (*Palaeocypraea*) *wilfredi* new species, holotype, LACMIP 13065, from LACMIP loc. 17611, 35.8 mm length. **Figures 4, 5.** *Bernaya* (*Bernaya*) *jeanae* new species, holotype, LACMIP 13067, from LACMIP loc. 17611, 42.4 mm length. **Figures 6–9.** *Bernaya* (*Bernaya*) *beardi* new species, holotype RBCM.EH2003.008.0001, from Vancouver Island, British Columbia, 36.7 mm length. **Figures 10, 11.** *Bernaya* (*Protocypraea*) *popenoei* new species, holotype UCMP 154951, from UCMP loc. A3404, 31.4 mm length.

nine species and 10 subspecies of Cretaceous *Palaeocypraea s.s.* Of these, six are from North America and two are from the Pacific slope (Groves, 1990). *Palaeocypraea* (*Palaeocypraea*) *fontana* (Anderson, 1958) from the Lower Cretaceous (uppermost lower Albian), Budden Canyon Formation, Shasta County, California, is the earliest known cypraeoidean from the Western Hemisphere. Other North American species are from San Juan County, Washington, Navarro County, Texas, New Castle County, Delaware, and Dawson County, Montana (Groves, 1990).

Subgenus *Palaeocypraea* Schilder, 1928
Palaeocypraea (*Palaeocypraea*) *wilfredi* new species
(Figures 2–3)

Diagnosis: A *Palaeocypraea* of medium size, elongate shell, broad spire, fine dentition, fossula concave and smooth.

Description: Shell medium in size, slightly constricted anteriorly; maximum height and width near center; spire of medium height, partially covered by successive whorls; dorsum slightly flattened; aperture narrow, fairly

straight; denticulation fine with smooth interstices, outer lip with 18 teeth, inner lip with six teeth; outer lip with prominent anterior terminal ridge, forming slight marginal callus.

Comparison: The new species is most similar to *Palaeocypraea (Palaeocypraea) suciensis* (Whiteaves, 1895: 127–128, pl. 3, fig. 5) from the Upper Cretaceous (lower Campanian) Cedar District Formation, Nanaimo Group, Sucia Island, San Juan County, Washington. *Palaeocypraea (Palaeocypraea) wilfredi* is larger, has finer apertural dentition, a narrower aperture, shallower anterior and posterior canals, and a more cylindrical shape than *P. (P.) suciensis.*

Discussion: Although post-burial crushing has damaged part of the posterior dorsum, preservation is adequate enough for unequivocal generic and subgeneric assignments. *Palaeocypraea (P.) wilfredi* is the first cypraeoidean reported from the Chico Formation.

Material: The new species is represented by two specimens. The holotype is slightly crushed, with minor amounts of original-shell material missing. The paratype exhibits small amounts of original-shell material but prominently displays the spire. An anterior outer lip fragment that exhibits original shell material from LACMIP loc. 24081 is also attributable to the new species.

Type Material: Holotype LACMIP 13065, paratype LACMIP 13066. Holotype measures 35.8 mm in length, 20.7 mm in width, and 17.0 mm in height. Paratype measures 34.8 mm in length, 20.6 mm in width, and 16.6 mm in height.

Type Locality: LACMIP loc. 17611, along Dry Creek, near Pentz, Butte County, California. Upper Cretaceous (lower Campanian), informal Pentz Road member, Chico Formation.

Etymology: Named after Wilfred Göhre (father of Eric Göhre, who collected and donated the type material to LACMIP) of Oroville, California.

Tribe Bernayini Schilder, 1927
Genus *Bernaya* Jousseaume, 1884

Type Species: *Cypraea media* Deshayes, 1835, by original designation. Upper middle Eocene (Bartonian Stage), Auvers-sur-Oise, Val-d'Oise, France.

Diagnosis: Shell medium to large in size, anterior end somewhat carinate, dorsum smooth, spire of medium height and partially covered by successive whorls, aperture wide, sides rounded, anterior and posterior canals deep, fossula smooth, concave, wide.

Remarks: Schilder and Schilder (1971) recognized six species and two subspecies of Cretaceous *Bernaya s.s.* Only one of these is from North America; *Bernaya (Bernaya) burlingtonensis* (Schilder, 1932) from the Upper Cretaceous (upper Campanian), Mt. Laurel-Navesink Formation, Burlington County, New Jersey. Groves (1990) described *B. (B.) crawfordcatei,* the first reported *Bernaya s.s.* from the Pacific slope, from the Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian), Point Loma Formation, near Carlsbad, northern San Diego County, California.

Bernaya (Bernaya) jeanae new species
(Figures 4–5)

Diagnosis: A *Bernaya* of medium size, anterior and posterior canals deep, spire of medium height, fossula smooth, concave, anterior and posterior terminal ridges prominent extending to margins.

Description: Shell medium in size, constricted anteriorly; maximum height and width posterior to center; spire of medium height, partially covered by successive whorls; aperture wide, straight; denticulation faint, outer lip with 13 teeth, teeth absent from inner lip; outer lip with prominent anterior and posterior terminal ridges extending to margins forming slight marginal callus.

Comparison: The new species is most similar to *Bernaya (Bernaya) crawfordcatei* Groves, 1990: 278, figs. 17–18, from the Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian), Point Loma Formation, San Diego County, California. *Bernaya (Bernaya) jeanae* is smaller in size, has finer apertural dentition, less prominent anterior and posterior basal ridges, and a less sinuous aperture than *B. (B.) crawfordcatei.*

Discussion: Post-burial crushing has damaged parts of the aperture and dorso-ventrally distorted the type material. Generic and subgeneric assignment are based on the wide aperture, deep anterior and posterior canals, and medium-height spire. Along with *Palaeocypraea (P.) wilfredi* (described above), this is the second cypraeoidean described from the Chico Formation.

Material: The new species is represented by the well preserved holotype and paratype, both of which exhibit original-shell material. Topotypic material includes 14 specimens in the collection of Eric Göhre, Oroville California, with varying amounts of original shell material. A single outer lip fragment from LACMIP loc. 24081 is assigned to the new species. A poorly preserved internal mold from the Chico Formation at the Granite Bay subdivision, Placer County, California (SC MG135) is attributable to the new species. An unusually large, poorly preserved specimen from Dry Creek near Pentz that measures 115.2 mm in length, 72.3 mm in width, and 38.7 mm, is tentatively identified as the new species.

Type Material: Holotype LACMIP 13067, paratype LACMIP 13068. Holotype measures 42.4 mm in length, 29.4 mm in width, and 19.8 mm in height. Paratype measures 47.1 mm in length, 30.6 mm in width, and 21.5 mm in height.

Type Locality: LACMIP loc. 17611, along Dry Creek, near Pentz, Butte County, California. Upper Cretaceous

(lower Campanian), informal Pentz Road member, Chico Formation.

Etymology: Named after Jean Göhre (mother of Eric Göhre, who collected and donated the type material to LACMIP) of Oroville, California.

Bernaya (*Bernaya*) *beardi* new species
(Figures 6–9)

Bernaya crawfordcatei Groves, 1990: Ludvigsen and Beard, 1994: 93, fig. 58 (left 2 figs.). Ludvigsen and Beard, 1997: 113, fig. 69 (left 2 figs.).
Bernaya (*Bernaya*) n. sp.: Groves, 1997: 7.

Diagnosis: A *Bernaya* of medium size, spire of medium height, aperture wide; fossula smooth, concave, anterior terminal canal deep.

Description: Shell medium in size; maximum height and width slightly posterior to center; spire of medium height, partially covered by successive whorls; aperture wide, straight; denticulation coarse with smooth interstices, outer lip with 13 teeth, teeth obsolete from inner lip; outer lip with weak posterior terminal ridge forming slight callus; marginal callus extends toward dorsum from outer and inner lip margins, forming coarse denticular pattern.

Comparison: The new species is unlike any known species of *Bernaya* (*B.*) in the Western Hemisphere although it superficially resembles *B.* (*B.*) *azevedoi* (Oliveira, 1957: 20, pl. 2, figs. 1, 3) from Upper Cretaceous (Maastrichtian) strata, Pernambuco State, Brazil and, *B.* (*Protocypraea*) *argonautica* (Anderson, 1958: 177, pl. 21, figs. 4–4a) from Upper Cretaceous (Cenomanian to Turonian) Hornbrook Formation, Osburger Gulch Sandstone Member (of Nilsen, 1984), Jackson County, Oregon. However, both species are markedly smaller than *B.* (*B.*) *beardi* and both are poorly preserved internal molds with little original-shell material preserved.

Discussion: Post-burial processes have removed much of the original-shell material from the dorsal surface of the holotype and the anterior terminal canal area is missing due to mechanical breakage. Generic and subgeneric assignments are based on the wide aperture, deep-posterior terminal canal, and spire of medium height. The unusual coarse marginal denticular pattern could be natural or an artifact of erosional processes. If this denticular pattern is indeed natural, it is unprecedented amongst cypraeids. Only species of the Eocene to Recent genus *Nucleolaria* Oyama, 1959, some members of the Recent genus *Cypraeovula* Gray, 1824, the Miocene to Recent species *Ipsa childreni* (Gray, 1825), and the Pleistocene to Recent species *Erosaria guttata* (Gmelin, 1791), have any outwardly similar marginal sculpture. *Bernaya* (*B.*) *beardi* appears to represent the northernmost record for a Cretaceous cypraeid worldwide. However, recent paleomagnetic paleolatitudinal studies by Kodama and Ward (2001) indicate that deposition of Nanaimo Basin sediments may have occurred at or around 40° N latitude (northern California) and transported northward in the post Late-Cretaceous. Enkin et al. (2001) concluded that the Nanaimo Basin was deposited near the present day California-Mexico border also based on paleomagnetic evidence. They also noted that this interpretation conflicts with sedimentologic and paleontologic evidence established by Elder and Saul (1993) and Haggart (2000) that the Nanaimo Basin was deposited near its present northern position.

Material: Represented by a well preserved holotype and three slightly juvenile topotypic specimens (VIPM 144, 146, and 147), all of which exhibit varying amounts of original shell material.

Type Material: Holotype RBCM.EH2003.008.0001 (*ex* VIPM 148), 36.7 mm in length, 28.9 mm in width, and 21.4 mm in height.

Type Locality: Near Brannen Lake, Vancouver Island, British Columbia, Canada, Upper Cretaceous (uppermost Santonian to lowermost Campanian), upper Haslam Formation, Nanaimo Group.

Etymology: Named after Graham Beard, founder of the Vancouver Island Paleontological Museum, Qualicum Beach, Vancouver Island, British Columbia, Canada.

Subgenus *Protocypraea* Schilder, 1927

Type Species: *Eocypraea orbignyana* Vredenburg, 1920 by original designation. Upper Cretaceous (Turonian through Santonian), Trichinopoly Group, Kullygoody, southern India.

Diagnosis: Shell small to medium in size, shape moderately pyriform, somewhat constricted anteriorly; fossula smooth, concave, wide.

Remarks: Schilder and Schilder (1971) recognized eight species and seven subspecies of Cretaceous *Bernaya* (*Protocypraea*). Two of their species [*B.* (*P.*) *argonautica* and *B.* (*P.*) *berryessae* both (Anderson, 1958)] and one subspecies, now recognized as a full species [*B.* (*P.*) *gualalaensis* (Anderson, 1958)], are from the Pacific slope of North America. Groves (1990) described *B.* (*P.*) *rineyi* from the Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian), Point Loma Formation, near Carlsbad, northern San Diego County, California. The only other North American species, *Bernaya* (*Protocypraea*) *mississippiensis* Groves (1990), is from the Upper Cretaceous (Campanian), Coffee Formation, Lee County, Mississippi.

Bernaya (*Protocypraea*) *popenoei* new species
(Figures 10–11)

Bernaya (*Protocypraea*) n. sp: Groves, 1997: 7.

Diagnosis: Pyriform *Protocypraea*, posterior terminal ridges forming slight marginal callus; fossula concave, smooth.

Description: Shell of medium size, moderately inflated, elongate and somewhat constricted anteriorly; spire partially covered by successive whorls; dorsum moderately arched; maximum height and width slightly posterior of center; aperture somewhat straight, narrow; teeth absent from both outer and inner lips; fossula concave, smooth, wide; posterior basal terminal ridges forming slight marginal callus; anterior and posterior terminal canals shallow.

Comparison: The new species is most similar to *Bernaya* (*Protocypraea*) *gualalaensis* (Anderson, 1958: 176, pl. 62, figs. 8–8a) from the Upper Cretaceous (upper Campanian to lower Maastrichtian) Gualala Formation, informal Anchor Bay member of Wentworth (1966) (see also Elder et al., 1998), Mendocino County, northern California. *Bernaya* (*Protocypraea*) *popenoei* is smaller than *B.* (*P.*) *gualalaensis* and has a narrower and straighter aperture, and more globose shape.

Discussion: Good preservation of the holotype permits unequivocal generic and subgeneric assignments. Although the Upper Cretaceous rocks of the Santa Ana Mountains, Orange County, California contain abundant mollusks (Packard, 1922; Popenoe, 1937, 1942; Saul, 1982, 1996), *B.* (*P.*) *popenoei* is the only cypraeoidaen so far described from the Ladd Formation.

Material: Represented by a single well preserved specimen that exhibits original-shell material.

Type Material: Holotype, UCMP 154951, measures 31.4 mm in length, 20.2 mm in width, and 17.8 mm in height.

Type Locality: UCMP loc. A3404, Lucas Canyon, Santiago Peak quadrangle, Santa Ana Mountains, Orange County, California, Upper Cretaceous (lower Campanian), Ladd Formation, Holz Shale Member.

Etymology: Named for the late Willis Parkinson ("Parky") Popenoe (University of California, Los Angeles), in recognition of his numerous significant contributions to Cretaceous paleontology and stratigraphy of the Santa Ana Mountains, Orange County, California.

NEW RECORDS OF PACIFIC SLOPE CRETACEOUS CYPRAEIDS

Bernaya (*Bernaya*) *crawfordcatei* Groves, 1990

New Record: LACMIP loc. 17198, west side of Bee Canyon, El Toro quadrangle (1949 ed.), Santa Ana Mountains, Orange County, California. Upper Cretaceous (upper lower Campanian), Williams Formation, Pleasants Sandstone Member. Poorly preserved internal mold.

Distribution: Formerly restricted to the *B.* (*B.*) *crawfordcatei* type locality (SDSNH loc. 3392), Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian), Point Loma Formation, near Carlsbad, northern San Diego County, California.

Bernaya (*Protocypraea*) *gualalaensis* (Anderson, 1958)

New Record: USGS Mesozoic loc. M8829 north side of Haven's Neck, Mendocino County, California. Upper Cretaceous (upper Campanian to lower Maastrichtian), Gualala Formation, informal Anchor Bay member. Two fairly well preserved internal molds were illustrated by Elder et al. (1998: 152, 163, pl. 1, figs. 2–3, 6).

Distribution: Type locality (CAS loc. 61918), near Gualala, Mendocino County, to the Carlsbad area, northern San Diego County, California (SDSNH locs. 3162, 3162-A, 3162-B, 3162-M, 3392, 3405, and 3454), Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian), Point Loma Formation.

Palaeocypraea sp.

New Record: LACMIP loc. 10441 (*ex* CIT loc. 1396). Sucia Island, San Juan County, Washington. Upper Cretaceous (lower Campanian), Cedar District Formation. Single, fairly well preserved, slightly dorso-ventrally crushed, juvenile specimen.

Cypraeidae, undetermined genus and species.

New Record: LACMIP loc. 17421, Palmer Way, Carlsbad, San Diego County, California. Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian) Point Loma Formation. Single poorly preserved internal mold.

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APPENDIX 1.

LOCALITIES CITED

CAS 61918 (*ex* S. G. Clark loc. 251). Near Gualala, sec. 27(?), T11N, R15W, MDMB, Gualala quadrangle, Mendocino County, California. Upper Cretaceous (upper Campanian to lower Maastrichtian), Gualala Formation. Coll.: S. G. Clark.

LACMIP 10441 (*ex* CIT loc. 1396). Bluffs along south side of Fossil Bay, south side and east end of Sucia Island, San Juan County, Washington. Upper Cretaceous (lower Campanian), Cedar District Formation. Coll.: R. Durbin, H. L. and W. P. Popenoe, 23 Jul, 1935.

LACMIP 17198. Unsorted very indurated conglomerate lens with pebble and cobble-sized clasts and a sandstone matrix; at elevation 207 m, on west side of divide on west side of Bee Canyon, 4496 m south and 3117 m east of northwest corner of USGS El Toro quadrangle (1949 ed.), Santa Ana Mountains, Orange County, California. Upper Cretaceous (upper lower Campanian), Williams Formation, Pleasants Sandstone Member. Coll.: P. Peck and others, 28 May, 1997. [Locality now inaccessible and covered by Eastern Transportation Corridor].

LACMIP 17421. In sandstone immediately overlying basal conglomerate and from spoil piles along south side of commercial property at 5607 Palmer Way, Carlsbad, San Luis Rey quadrangle (1975), San Diego County, California. Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian), Point Loma Formation. Coll.: G. L. Kennedy.

LACMIP 17611. Dry Creek, near Pentz, Butte County, California. Upper Cretaceous (lower Campanian), informal Pentz Road member, Chico Formation. Coll.: E. S. Göhre.

LACMIP 24081 (*ex* UCLA loc. 4081). South of Pentz, Butte County, California. Upper Creatceous (lower Campanian), informal Pentz Road member, Chico Formation. Coll.: T. Susuki.

SDSNH 3162. Carlsbad area, locality (now covered by Faraday Avenue) was exposed during development of Carlsbad Research Center, southwest of El Camino Real, south of Letterbox Canyon and north of Palomar Airport, 33°08′02″ N, 117°16′41″ W, San Luis Rey quadrangle, San Diego County, California. Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian), Point Loma Formation. Coll.: B. O. Riney, T. A. Deméré, and M. A. Roeder, Mar–May, 1982.

SDSNH 3162-A. Carlsbad area, at base of stratigraphic section measured at SDSNH 3162, approximately 6.1 m below a calcareous marker bed. Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian), Point Loma Formation. Coll.: B. O. Riney, T. A. Deméré, and M. A. Roeder, Mar–May, 1982.

SDSNH 3162-B. Carlsbad area, 2.1–3.9 m below a calcareous marker bed in measured stratigraphic section at SDSNH 3162. Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian), Point Loma Formation. Coll.: B. O. Riney, T. A. Deméré, and M. A. Roeder, Mar–May, 1982.

SDSNH 3162-M. Carlsbad area, near top of stratigraph-

ic section measured at SDSNH 3162. Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian), Point Loma Formation. Coll.: B. O. Riney, T. A. Deméré and M. A. Roeder.

SDSNH 3392. Carlsbad area, north of Palomar Airport, roadcut along west side of College Boulevard, approximately 424 m south of intersection with El Camino Real, 33°08′21″ N, 117°17′02″ W, San Luis Rey quadrangle, San Diego County, California. Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian), Point Loma Formation. Coll.: SDSNH field party May, 1987.

SDSNH 3405. Carlsbad area, north of Palomar Airport, excavation for College Boulevard, approximately 242–485 m south of intersection with El Camino Real, 33°08′21″ N, 117°17′02″ W, San Luis Rey quadrangle, San Diego County, California. Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian), Point Loma Formation. Coll.: B. O. Riney, M. A. Roeder, and R. Q. Gutzler, Apr–May, 1987.

SDSNH 3454. Carlsbad area, north of Palomar Airport, excavation for College Boulevard, approximately 153 m north of College Boulevard and Faraday Avenue intersection, 33°08′11″ N, 117°17′02″ W, San Luis Rey quadrangle, San Diego County, California. Upper Cretaceous (uppermost Campanian to lowermost Maastrichtian), Point Loma Formation. Coll.: B. O. Riney and M. A. Roeder, Apr–May, 1987.

UCMP A3404. Fossils in float boulders in Lucas Canyon, a branch of San Juan Canyon, near San Juan Capistrano, Santiago Peak quadrangle, Santa Ana Mountains, Orange County, California. Upper Cretaceous (lower Campanian), Ladd Formation. September, 1916.

USGS Mesozoic loc. M8829. Conglomerate at northeast end of beach on north side of Haven's Neck in SW¼ SW¼ SE¼, section 12, T11N, R16W, Mendocino County, California. Upper Cretaceous (upper Campanian to lower Maastrichtian), Gualala Formation, informal Anchor Bay member. Coll.: W. P. Elder, 1992.

Book Review

Checklist of the Land Snails and Slugs of California

Roth, B. and P. S. Sadeghian. 2003. Checklist of the Land Snails and Slugs of California. Santa Barbara Museum of Natural History Contributions in Science, Number 3, 81 pp., 13 color plates.

Creating lists is one of the most important things that systematists do. By bringing together in a single place nomenclatural, bibliographic, distributional, and type material information, such checklists or catalogs are fundamental to revisionary systematics, to biogeography, and to biodiversity conservation.

Checklists are primarily works of nomenclature in that they are compilations of names, with varying amounts of additional information associated with each name. They can be lists of all the names in a particular higher taxon (e.g., the family Partulidae—Richardson, 1990), although often they are also geographically constrained (e.g., the recent catalog of the New World Ampullariidae—Cowie and Thiengo, 2003). Some catalogs list all the names introduced by particular authors (e.g., those of Clench and Turner—Johnson, 2003), perhaps restricted to a higher taxon of interest (e.g., the Neritidae described by Récluz—Kabat and Finet, 1992). And some catalogs are compilations of all names in a particular fauna, as in the case of the present work on the land gastropod fauna of California. These last are the most valuable checklists for conservation because in order to conserve a fauna it is necessary to know as well as possible which species constitute that fauna. Checklists such as this one provide that essential baseline of knowledge.

In addition to being a compilation of all the names of land snails and slugs, including non-native species, known from California, this checklist includes details of name-bearing type material, and the county-by-county distributions of the recognized species and subspecies. Non-native species are clearly identified by asterisks. The checklist is also in a sense a work of taxonomy. Rather than listing all names separately, with no expressed opinion as to their synonymy, synonyms (including some new synonyms) are listed under the species/subspecies with which they are synonymized. The species are listed alphabetically under the appropriate genera, and genera are listed alphabetically under the appropriate higher taxa. Some new species/genus combinations are introduced.

A bonus, not often seen in such checklists, is the set of beautiful color plates illustrating, mostly for the first time, holotypes and lectotypes of 64 land snail taxa described by S. Stillman Berry and deposited in the Santa Barbara Museum of Natural History.

A total of 279 extant species and 112 subspecies are listed, plus 6 species known only as fossils, for an overall total of 397 valid taxa. Of these, 20 are as yet undescribed species and subspecies, and 37 are non-native species in California. Numerous synonyms are also listed. Distributional information is based on extensive research in museum and private collections. As is made clear, however, even a fauna that might be expected to be better known than many, in fact probably includes many species remaining to be discovered, including cryptic species that may only be discovered using molecular techniques; and field work will probably extend the recorded distributions of the known species beyond those reported in this checklist.

This is a valuable work that gives us just a tantalizing taste of what is to come in a manual of the land snails and slugs of California, currently in preparation by Roth. However, I cannot end without mentioning a very small number of essentially minor criticisms. First, I would have liked to have had an index—I went to find one particular genus and had to thumb through the book to locate it, but more importantly, the lack of an index makes it difficult to locate synonyms. Second, it would have been nice to have had a bibliography of the original descriptions, but this will no doubt be available in the forthcoming manual. Finally, I understand the logic behind the authors' reluctance to use 'formal [taxonomic] ranks above the genus', but in fact they do use the 'traditional names of taxa' above the genus throughout the checklist, which allows the more traditional among us to follow it. Among the Helminthoglyptidae, however, they also use Roth's (1996) rather obscure hierarchical cladistic nomenclature—difficult to understand in part because, given the way the book is laid out, it is difficult to see how far the various clade names are indented, which is crucial to understanding their relationships. But these are quibbles. This is a useful and important book, both for systematists working with the groups represented in California, and especially as a foundational documentation of California's biodiversity that will be an important tool in its conservation.

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CONTENTS

John Slapcinsky
Brian Coles
Revision of the genus *Pilsbryna* (Gastropoda: Pulmonata: Gastrodontidae) and comments on the taxonomic status of *Pilsbryna tridens* Morrison, 1935 55

Robert H. Cowie
Néstor J. Cazzaniga
Matthias Glaubrecht
The South American Mollusca of Johann Baptist Ritter von Spix and their publication by Johann Andreas Wagner 71

Sven N. Nielsen
The genus *Olivancillaria* (Gastropoda: Olividae) in the Miocene of Chile: rediscovery of a senior synonym and description of a new species 88

Sponsored in part by the State of Florida, Department of State, Division of Cultural Affairs, the Florida Arts Council and the National Endowment for the Arts.

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Revision of the genus *Pilsbryna* (Gastropoda: Pulmonata: Gastrodontidae) and comments on the taxonomic status of *Pilsbryna tridens* Morrison, 1935

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ABSTRACT

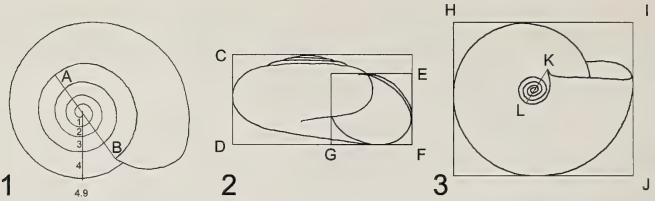
Pilsbryna is revised based on new material collected during recent surveys of wet leaf-litter microhabitats in the southern Appalachian Mountains. Five species are recognized including *Pilsbryna aurea* Baker, 1929, *P. castanea* Baker, 1931, *P. nodopalma* new species and *P. quadrilamellata* new species. All species are redescribed or described. *Pilsbryna vanattai* (Walker and Pilsbry, 1902) is transferred to *Pilsbryna* from *Glyphyalinia* (*Glyphyalus*) based on genital and juvenile shell anatomy. *Pilsbryna tridens* Morrison, 1935, is reexamined based on newly available material; its placement in the genus *Helicodiscus* sensu lato is supported by new radular evidence. *Pilsbryna* species share unique genital and shell characteristics that are included in a redescription of the genus. The new generic definition combined with habitat information for all *Pilsbryna* species allows a better understanding of the geographic and microhabitat distribution of the genus.

INTRODUCTION

Although the terrestrial invertebrate fauna of eastern North America is among the best known in the world, new species are discovered frequently. Most are small species from patchily distributed and poorly sampled microhabitats. Recent collecting in one such habitat, damp to wet leaf-litter surrounding mountain seeps, springs and streams, has uncovered a remarkable radiation of small terrestrial snails of the genus *Pilsbryna*. In this paper, we redescribe the genus, describe two new species of *Pilsbryna*, and redescribe the other three species in the genus including a species formerly placed in the genus *Glyphyalinia*. One other previously described species, *P. tridens*, was reassigned to *Helicodiscus* by Hubricht (1964) without explanation. This generic placement was used in most subsequent publications listing the species (Riedel, 1980; Hubricht, 1985; Turgeon et al., 1988, 1998) although it has remained unconfirmed until now. Newly collected material of *H. tridens* allows for its unequivocal generic assignment.

MATERIALS AND METHODS

Specimens were hand-collected from the leaf-litter/soil interface or sifted from samples of leaf-litter. Live collected animals were narcotized overnight in a suspension of water containing a 1 cm length of mentholated cigarette and then preserved in 75% ethanol. Gross anatomical dissections were made under 75% ethanol using a dissecting microscope. Isolated reproductive systems were stained with Harris haematoxylin and Semichon aceto-carmine stain and cleared with glycerin. Radulae were isolated from dissected buccal masses using a saturated KOH solution. Scanning electron micrographs of shells and radulae were made using a field emission-SEM. Drawings of the shell and genital anatomy were made with the assistance of a camera lucida, and measurements were taken using an ocular micrometer. All line drawings of the internal structures of juvenile shells are in basal view and use solid lines for shell outlines and internal structures that make contact with the inner surface of the translucent base of the shell. Dotted lines indicate structures that are viewed through the translucent base of the shell but do not make contact with the base. Shell measures were made as follows. Whorl count (W) was measured from the suture of the first whorl to the body whorl (Figure 1) and fractions of a whorl were determined with the aid of a cardboard circle divided into 10 equal parts of 36°. Spire diameter (SD) was measured as the length of a straight line passing from the apertural edge of the suture through the middle of the apex to the opposite suture (Figure 1, line a–b). Height (H) was the greatest distance between the apex and the base of the aperture measured parallel to the shell axis (Figure 2, line c–d). Aperture height (AH) was measured from the suture to the base of the aperture, parallel to the shell axis (Figure 2, line e–f). Aperture width (AW) was the greatest distance from the apertural edge of the umbilicus to the outer edge of the aperture (Figure 2, line g–f). Greater diameter (GD) was the measure of the greatest width of the shell (Figure 3, line h–i), and lesser diameter (LD) was the diameter perpendicular to



Figures 1–3. Shell measurements: **1.** Whorl count (1–4.9), spire width (line A–B). **2.** Shell height (line C–D), aperture height (line E–F), aperture width (line F–G). **3.** Greater diameter (line H–I), lesser diameter (line I–J), umbilical width (line K–L).

the greater diameter (Figure 3, line i–j). Umbilical Width (UW) was measured from the inner edge of the aperture through the center of the umbilicus to the opposite side of the umbilicus (Figure 3, line k–l). Maps were made with the assistance of DeLorme, Topo USA software. We examined specimens of *Pilsbryna* in the collections of the Academy of Natural Sciences, Philadelphia (ANSP), Field Museum of Natural History, Chicago (FMNH), North Carolina State Museum, Raleigh (NCSM), National Museum of Natural History (USNM) and Florida Museum of Natural History, Gainesville (UF) and the private collection of one of the authors (BC).

The following abbreviations are used in figures of genital anatomy: AG = albumen gland, EP = epiphallus, HD = hermaphroditic duct, OV = free oviduct, PE = penis, PG = prostate gland, PP = penial papillae, PR = penial retractor muscle, SD = spermathecal duct, SP = spermatheca, UT = uterus, VD = vas deferens. Anatomical terminology follows Pilsbry (1946); for alternate usages see Tompa (1984).

SYSTEMATICS

Family Gastrodontidae Tryon, 1866
Genus *Pilsbryna* Baker, 1929

Type Species: *Pilsbryna aurea* Baker, 1929 by monotypy.

Description: Small snails of the family Gastrodontidae with depressed-helicoid and umbilicate shells of roughly 5 whorls that are sculptured with closely placed, shallow axial grooves. Whorl expansion is slow and regular through the penultimate whorl and more rapid in the body whorl. Shells of juveniles usually contain spirally arranged lamellae or nodules within the shell. These lamellae or nodules occur at mid parietal and various other positions from columellar to sutural, and are reduced or completely resorbed in adult shells.

The apical ⅓ to ½ of the penis bears papillae that are not located within a well-defined apical chamber. The base of the penis is thin-walled and simple. The penial retractor muscle is inserted near the apex of the penis. The epiphallus is robust, of similar diameter to the penis, does not bear a caecum and joins the penis laterally at the apex. The epiphallus is well defined at the junction with the vas deferens. The spermathecal duct is long and slender and the spermatheca ovate. There are no well-defined glandular areas within the free oviduct.

The form of the radula is typical of many small North American Gastrodontidae. The centrals are symmetric and tricuspid and of similar height to the first laterals. There are three asymmetric tricuspid laterals on each side of the central, and numerous unicuspid marginals.

Remarks: *Pilsbryna* has been treated as a subgenus of *Paravitrea* by Riedel (1980); however, similarities between the two genera are superficial or shared by several other groups of North American Gastrodontidae. Although both *Pilsbryna* and *Paravitrea* possess internal barriers in the shell, the form and position of these barriers differs. Juvenile *Pilsbryna* possess spiral lamellae or series of nodules, usually at the parietal, palatal and basal positions. *Paravitrea* species usually have axial rows of two to many, evenly spaced, small lamellae grouped ¼ to ⅓ whorl apart that are not concentrated near the aperture. The shells of *Paravitrea* are more tightly coiled, usually with 6 or more whorls while shells of *Pilsbryna* attain fewer than 6 whorls and more closely resemble those of some *Glyphyalinia* and *Nesovitrea*. Analysis of genital characters also does not support the placement of *Pilsbryna* within the genus *Paravitrea*. The genital anatomy of all known species of *Pilsbryna* is highly conserved and the combination of genital characters found in *Pilsbryna* are not found in *Paravitrea* or in any other group of North American Gastrodontidae. Similarities in radular anatomy between *Pilsbryna* and *Paravitrea* are not unique; they are shared with most small American Gastrodontidae, including *Glyphyalinia* and *Nesovitrea*. The unique apertural barriers of the shell, the rows of papillae at the apex of the penis and the unusual habitat shared by *Pilsbryna* species strongly suggest the group is monophyletic and distinct from other genera of small American Gastrodontidae. In any case, evidence of a particularly close relationship between *Pilsbryna* and *Paravitrea* is lacking, and *Pilsbryna* is here considered a distinct genus.

Pilsbryna aurea Baker, 1929
Common name: ornate bud
(Figures 4–10, Table 1)

Pilsbryna aurea Baker, 1929a: 91–92, pl. 3, figs. 4–8; Baker, 1929b: 260–261, pl. 9, figs. 4–5; Baker, 1931: 112–113, pl. 19, figs. 9–13, pl. 20, fig. 5; Pilsbry, 1946: 389–391, fig. 205(4–5), fig. 206(a–c), fig. 207(9–13), fig. 208(5); Baker, 1962: 3; Burch, 1962: 107, fig. 257; Hubricht, 1973: 14; Turgeon et al., 1988: 135; Turgeon et al., 1998: 148.

Diagnosis: A medium-sized *Pilsbryna* with an adult shell diameter of 2.9–3.6 mm, height of 1.4–1.9 mm and 5.0–5.4 whorls. Shells of less than 3.5 whorls contain two lamellae, one crescent-shaped at mid-columellar position, the second blade-shaped or undulate at mid-parietal position. Both lamellae extend up to ⅓ whorl into the body whorl. The parietal lamella is often thickened along its distal edge giving it a T-shaped cross section.

Description: Shell depressed-helicoid, umbilicate, glossy, translucent and densely sculptured with irregularly spaced, indented axial lines (Figures 4–6). Adult shell (Table 1) about 2.9–3.6 mm (mean = 3.2, n = 10) in major diameter and 1.4–1.9 mm (mean = 1.7) in height with 5.0–5.4 (mean = 5.1) slowly expanding whorls. The shell height/greater diameter ratio is 0.48–0.56 (mean = 0.52) and the spire width/greater diameter ratio is 0.53–0.60 (mean = 0.57). The final ⅓ of the body whorl expands slightly more rapidly than previous whorls; the lesser/greater diameter ratio is 0.82–0.91 (mean = 0.86). The aperture is ovate, widest at or slightly below the middle of the whorl. The umbilicus is 0.4–0.6 mm (mean = 0.5) in diameter and 0.13–0.19 (mean = 0.16) of the greater diameter of the shell. The funnel shaped umbilicus expands regularly until the final third of the body whorl, where it expands more rapidly. Shells of immature animals contain two lamellae, a crescent shaped lamella at mid-columellar position and an undulating lamella at mid-parietal position (Figures 7–8). Both lamellae extend up to ⅓ whorl into the aperture. The parietal lamella is usually thickest distally and is often T shaped in cross section. Both lamellae are much reduced and more often completely resorbed in adults.

The basal half of the penis is straight-sided and simple while the apical half is robust, bearing numerous small papillae (Figure 9). The penial retractor muscle is subapically inserted. The epiphallus is about the same length and roughly half the diameter of the penis and inserts laterally at the apex of the penis. The diameter of the epiphallus remains roughly constant and widens only slightly at the junction with the narrow vas deferens. The epiphallus is folded at the mid-point and also has longitudinal folds internally. The spermatheca is ovate, and the narrow spermathecal duct expands very slightly basally. The free oviduct is roughly twice the diameter of the base of the penis, expanding slightly at the junction with the spermathecal duct. A caecoid outpocketing was not observed on the free oviducts of two dissected adults.

The central tooth of the radula is symmetrically tricuspid; the mesocone is slender, especially basally, expanding slightly above the ectocone cusps and then tapers slowly to the apex (Figure 10). The ectocones are short, roughly ⅓ the total height of the tooth, symmetrical and diamond-shaped. The three laterals are tall, slender, and asymmetrically tricuspid. The endocone is tall about ⅔ the height of the mesocone. The ectocone is ⅓ the height of the mesocone and separated from it by a narrow gap. The marginals are tall, slender and unicuspid, with concave peripheral edges and convex proximal edges. We studied two radulae (UF 287063) using SEM microscopy. Both had twenty marginals on each side.

Holotype: ANSP 147189a. Baker (1929a) figured and measured this shell and designated it as the type, thereby fixing the holotype.

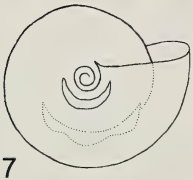
Paratypes: ANSP 147189, type locality, Baker, 1928.

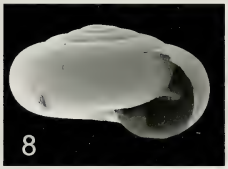
Type Locality: USA, Tennessee, Unicoi County, Limestone Cove, Big Springs, between Unaka and Stone Mountains, about 11 km E of Unicoi, 36° 11′ N, 82° 17′ W, elevation 700 m, Baker, 1928.

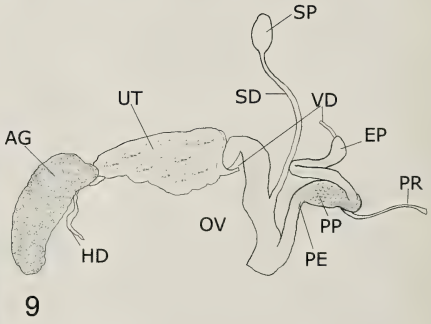
Other Material Examined: ANSP 158890, USA, Tennessee, Unicoi County: Limestone Cove; ANSP 152469, type locality, Baker, 1928; ANSP 165583, Baker, 26–30 Aug. 1928; UF 292089, UF 287063, Davis Springs, 8 km E of Unicoi, 36°10.7′ N, 82°16.4′ W, 687 m elevation, J. Slapcinsky and B. Coles, 31 May 2001; FMNH 248868, near Davis Springs, 8 km E of Unicoi, L. Hubricht, 18 May 1961; FMNH 248867, 2.1 km SE of Limestone Cove, L. Hubricht, 28 May 1974; BC 6761, Washington County, Dry Creek Road, 1 km S of Jim McNeese Road, 36° 15.6′ N, 82° 21.9′ W, 637 m elevation, B. Coles, 21 May 2002.

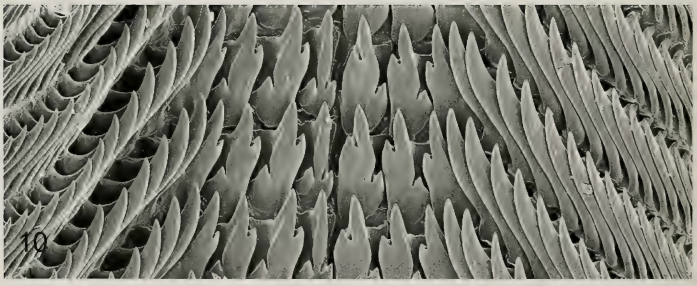
Remarks: Several characters of the genital and radular anatomy differed from previously published descriptions. A caecoid outpocketing was not observed on the free oviducts of two adults dissected in this study; in contrast, Baker (1929b) recorded it in a juvenile. However, reproductive structures, especially those of the posterior portion of the reproductive system, can vary in size, shape, color and texture with maturation and reproductive stage (Emberton, 1985). Our observations of the structures of the anterior portion of the reproductive system compare well with those of Baker (1929b). This study using SEM microscopy found twenty marginals per side. In contrast, Baker (1929b), using light microscopy, recorded only 14 marginals in an immature specimen.

Pilsbryna aurea appears most similar to *Pilsbryna quadrilamellata* described below, juvenile shells of these two share unique crescent-shaped columellar lamellae and lack spiral rows of nodules at any position. However, the two species are easily separated using other juvenile shell characters: *P. aurea* has a distally expanded parietal lamella and does not possess the mid-basal and sutural lamellae of *P. quadrilamellata*. Anatomically, *P. aurea* can









Figures 4–10. *Pilsbryna aurea.* **4–6.** UF 287063, diameter 3.2 mm. **7.** FMNH 248868, diameter 2.6 mm. **8.** UF 287063, diameter 2.1 mm. **9.** Camera lucida drawings of genitalia, UF 292089, maximum width 5.9 mm; **10.** UF 292089, horizontal field width = 217 μm.

Table 1. Measurements in mm of undamaged adult shells of five species of *Pilsbryna*, N = 10. GD = greater diameter, LD = lesser diameter, H = height, AW = aperture width, AH = aperture height, SW = spire width, UW = umbilicus width, W = number of whorls.

		GD	LD	H	AW	AH	SW	UW	W
P. aurea	Mean ± SD	3.2 ± 0.2	2.8 ± 0.2	1.7 ± 0.2	1.5 ± 0.1	1.3 ± 0.1	1.8 ± 0.1	0.5 ± 0.1	5.1 ± 0.1
	Range	2.9–3.6	2.5–3.0	1.4–1.9	1.3–1.7	1.2–1.4	1.7–2.0	0.4–0.6	5.0–5.4
P. castanea	Mean ± SD	3.7 ± 0.2	3.2 ± 0.1	2.0 ± 0.1	1.7 ± 0.1	1.5 ± 0.1	2.1 ± 0.1	0.7 ± 0.1	5.2 ± 0.2
	Range	3.5–3.9	3.0–3.4	1.9–2.2	1.6–1.8	1.4–1.6	2.0–2.3	0.6–0.8	5.0–5.4
P. nodopalma	Mean ± SD	3.0 ± 0.1	2.6 ± 0.1	1.5 ± 0.1	1.4 ± 0.1	1.2 ± 0.1	1.7 ± 0.1	0.5 ± 0.1	4.5 ± 0.1
	Range	2.7–3.1	2.4–2.8	1.4–1.6	1.3–1.5	1.2–1.3	1.6–1.8	0.4–0.5	4.3–4.6
P. quadrilamellata	Mean ± SD	3.2 ± 0.2	2.8 ± 0.2	1.7 ± 0.1	1.5 ± 0.1	1.3 ± 0.0	1.9 ± 0.1	0.5 ± 0.1	5.0 ± 0.2
	Range	2.8–3.4	2.5–3.0	1.5–1.8	1.4–1.6	1.3–1.4	1.8–2.2	0.4–0.6	4.7–5.2
P. vanattai	Mean ± SD	4.0 ± 0.2	3.4 ± 0.2	2.0 ± 0.1	2.0 ± 0.2	1.7 ± 0.1	2.0 ± 0.1	0.5 ± 0.1	4.8 ± 0.2
	Range	3.8–4.4	3.2–3.7	1.9–2.2	1.8–2.3	1.5–1.9	1.9–2.3	0.5–0.6	4.6–5.1

be distinguished from other species of *Pilsbryna* by the unusually inflated apex of its penis and by the clearly subapical insertion of its penial retractor muscle. The teeth of the radula are tall and slender. The central tooth is especially slender, and unlike other *Pilsbryna* species, does not bear a strong angle at its widest point. The peripheral ectocones are relatively poorly defined, separated from the adjacent mesocone by narrow gaps similar to those of *P. castanea* and *P. nodopalma*, described below, and unlike those of *P. quadrilamellata* and *P. vanattai*.

Habitat and Distribution: Previously, *Pilsbryna aurea* was known from sites within 3 km of the town of Limestone Cove in Unicoi County, Tennessee (Baker, 1929a; Hubricht, 1973). Recent collecting has also uncovered this species along Dry Creek Road, south of Johnson City, a range extension of more than 10 km to the northwest. This species appears to be restricted to mountain valleys near Unicoi, Tennessee, and has been found at elevations of 600–700 m. Known populations occur on rocky wooded hillsides along small streams. The species is most common in wet leaf-litter along streams and around seeps but is also found in deep leaf-litter at the base of limestone and other sedimentary rocks along stream banks.

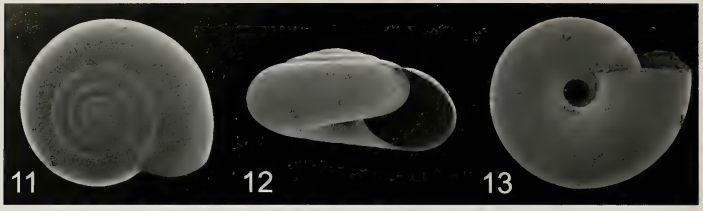
Pilsbryna castanea Baker, 1931
Common name: prominent bud
(Figures 11–17, Table 1)

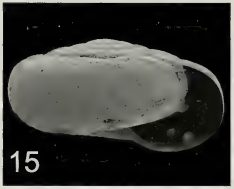
Pilsbryna castanea Baker, 1931: 111–112, pl. 19, figs. 1–8, pl. 20, fig. 4; Pilsbry, 1946: 391–393, fig. 207(1–8), fig. 208(4); Baker, 1962: 5; Burch, 1962: 94, 98, 106, fig. 219, fig. 228, fig. 256; Hubricht, 1973: 14; Turgeon et al., 1988: 135; Turgeon et al., 1998: 148.

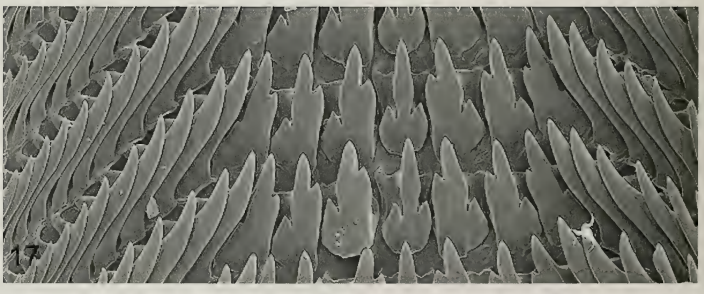
Diagnosis: A medium to large *Pilsbryna* with an adult shell diameter of 3.4–3.9 mm, height of 1.9–2.2 mm, and whorl count of 5.1–5.4 whorls. Shells with fewer than 4 whorls have a sinuous parietal lamella and a spiral series of basal nodules extending a full whorl into the aperture. Shells 4.5 whorls contain only a few basal nodules roughly half way into the body whorl and all traces of lamellae are resorbed in most adults.

Description: The shell is depressed-helicoid and umbilicate, with its surface sculptured with dense and irregularly spaced axial indentations (Figures 11–13). *Pilsbryna castanea* is relatively high-spired (Table 1), with a shell height of 1.9–2.2 mm (mean = 2.0, n = 10), width of 3.4–3.9 mm (mean = 3.7) and height/width ratio of 0.51–0.58 (mean = 0.55). The shell is relatively tightly coiled with 5.1–5.4 (mean = 5.2) whorls; the final ⅓ of the body whorl expands slightly more rapidly than previous whorls and the ratio of lesser/greater diameter is 0.82–0.89 (mean = 0.86). The spire is 0.55–0.61 (mean = 0.58) of the greater diameter. The umbilicus is relatively straight-sided and 0.6–0.8 mm (mean = 0.7) wide; the ratio of umbilical width/greater diameter is 0.17–0.21 (mean = 0.19). Juvenile shells with fewer than four whorls usually have a mid-parietal lamella and a spiral row of low nodules at basal position (Figures 14–15). Both often extend a full whorl or more into the aperture. The position of the basal nodules coincides with the summits of the undulating parietal lamella. Animals with shells more than four whorls gradually stop producing lamellae and begin to resorb previously deposited lamellae. The shells of animals approaching maturity often contain traces of the lamellae a half whorl into the aperture; by the time most animals reach maturity all traces of apertural barriers are resorbed.

The penis is narrow and elongate, slightly constricted above the base, expanding slowly apically, widest ⅔ from the base, then tapering slowly to the apex (Figure 16). The apical half bears small papillae. The penial retractor muscle is inserted nearly apically. The epiphallus is longer than the penis, and joins it laterally at the apex. The epiphallus is narrowest near the junction with the penis is folded at mid-point, and slightly inflated towards the vas deferens. The vas deferens is narrow; the junction with the much wider epiphallus is well defined. Free oviduct is slightly wider than the penis, where they meet and widens at and above the attachment of the sper-







Figures 11–17. *Pilsbryna castanea.* **11–13.** UF 297381, diameter 3.6 mm. **14.** UF 297381, diameter 2.6 mm. **15.** UF 297381, diameter 2.4 mm. **16.** Camera lucida drawings of genitalia, UF 297419, maximum width 5.8 mm. **17.** UF 297419, horizontal field width 205 μm.

mathecal duct. Spermathecal duct is long and narrow; the spermatheca is ovate. One animal was dissected.

The central tooth of the radula is tall, slender and tricuspid (Figure 17). The mesocone is elongate, widest and angular slightly above the ectocone cusps and tapering sharply towards the apex and narrowing towards the base. The ectocones are slightly less than ½ the total height of the tooth, symmetrical, and diamond-shaped. The three lateral teeth are tall, slender and asymmetrically tricuspid. The endocone of each is tall and the ectocone short. The seventeen marginal teeth on each side are tall, slender and unicuspid, with concave peripheral, and convex proximal, edges. One radula was examined.

Holotype: ANSP 152468a. Baker (1931) figured and measured this shell and designated it the type, thereby fixing the holotype.

Paratypes: ANSP 152468, type locality.

Type Locality: USA, Tennessee, Marion County, Dove, mouth of Cave Cove, west facing hillside south of big spring, which forms eastern source of Battle Creek, 35°10′ N, 85°47′ W, 244 m elevation, Baker, 1931.

Other Material Examined: ANSP 165582, USA, Tennessee: Marion County, type locality, Baker, 23–26 Jul. 1928; FMNH 171387, west side of Battle Creek at junction of Ladd's Cove Road and Interstate 24, 35°8.7′ N, 85°46.7′ W, 193 m elevation, 4 Sep. 1974, G. Goodfriend; UF 297419, UF 297381, 9 Jun. 2002, J. Slapcinsky; FMNH 171403, Martin Springs 10 km south of Monteagle, 4 Sep. 1974, G. Goodfriend; FMNH 248870, 8 km N of Sequatchie, near large spring, 23 Oct. 1962, L. Hubricht; UF 306530, Bledsoe County, Lusk Loop Road, 0.5 km NW of Cannon Creek, 35°30.1′ N, 85°18.9′ W, 300 m elevation, 1 Jun. 2003, J. Slapcinsky; FMNH 171335, NE side of Rains Gulf, 18 km SW of Pikeville, 410 m elevation, 7 Sep. 1974, G. Goodfriend; ANSP 165581, Cannon Creek, W of Pikeville, 1928, H. B. Baker.

Remarks: Like *Pilsbryna nodopalma,* described below, and *P. vanattai,* juvenile *P. castanea* have spiral series of nodules. *Pilsbryna castanea* can be distinguished from the other two species because it does not possess a second series of nodules at the palatal position. The nodules are peg-shaped and not dorsoventrally compressed like those of *P. nodopalma.* The nodules in *P. castanea* can extend the entire body whorl, much farther than those of the other nodulate species. However, this last character is less useful when comparing older juveniles that have discontinued deposition of lamellae and have begun to resorb previously deposited barriers. The adult shells of *P. castanea* are larger than those of *P. nodopalma,* have a greater height/width ratio than *P. vanattai,* and have more whorls than either species.

Habitat and Distribution: *Pilsbryna castanea* is found on wooded hillsides bordering Battle Creek and the Sequatchie Valley in Marion and Bledsoe Counties, Tennessee (H.B. Baker, 1931; Pilsbry, 1948; Hubricht, 1973, 1985). All animals were found in deep leaf-litter at the base of limestone exposures. Live specimens are most common in wet leaf-litter surrounding seeps.

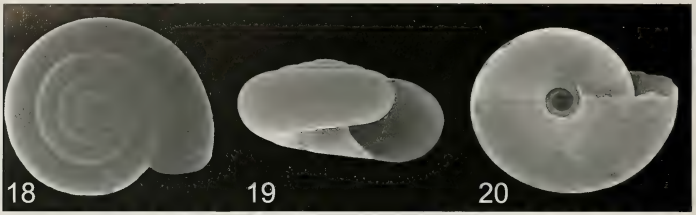
Pilsbryna nodopalma new species
Common name: oar tooth bud
(Figures 18–24, Table 1)

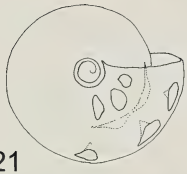
Pilsbryna (unidentified): Lee, 1990: 7–8, fig. (unnumbered)

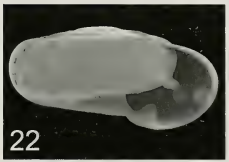
Diagnosis: A small and relatively loosely-coiled *Pilsbryna* of 2.7–3.2 mm diameter and 1.4–1.6 mm height, with 4.3–4.6 regularly expanding whorls. The shell whorls are widest above the middle. The shells of juvenile animals contain an undulate parietal lamella and three or four paired subcolumellar and lower palatal nodules grouped near the aperture. These nodules are dorsoventrally compressed.

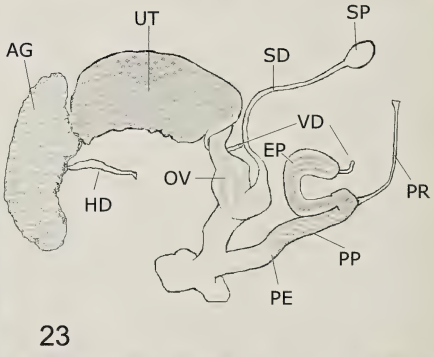
Description: The shell is depressed-helicoid, umbilicate and translucent. The shell is small and loosely coiled for the genus (Table 1); adults reach 2.7–3.2 mm (mean = 3.0, n = 10) greater diameter and 1.4–1.6 mm (mean = 1.5) height with 4.3–4.6 (mean = 4.5) whorls (Figures 18–20). Height is 0.47–0.53 (mean = 0.51) of the greater diameter. Whorl expansion is regular and increases only slightly in the last third of the body whorl; the ratio of lesser diameter to greater diameter is 0.83–0.90 (mean = 0.86). The shell surface is glossy and sculptured with weak and irregularly spaced indented axial lines. The apex is relatively flat and the whorls are widest slightly above mid-point. Spire width is 0.53–0.60 (mean = 0.58) of greater diameter. The sutures are relatively deeply impressed for the genus. The umbilicus is narrow, 0.4–0.5 mm (mean = 0.45) roughly 0.13–0.17 (mean = 0.15) of shell diameter. Juvenile shells, with less than four whorls, have an undulate parietal lamella and two to four, paired, subcolumellar and lower palatal nodules grouped near the aperture (Figures 21–22). These nodules are dorsoventrally compressed giving some of them the appearance of the tips of oar blades. The parietal lamella is undulate and is tallest where it passes the paired lower palatal and subcolumellar nodules. The distal edge of the parietal lamella points towards the lower palatal nodules.

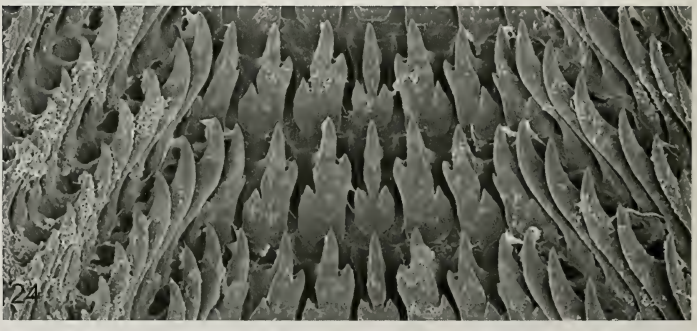
The penis is relatively short and moderately robust; it is apically papillate and basally smooth (Figure 23). The epiphallus is moderately short, about the same length and diameter as the penis. The penial retractor muscle is inserted nearly apically on the penis. The epiphallus is constricted slightly at the subapical junction with the penis and has strong internal longitudinal folds. The base of the spermathecal duct is robust with weak internal folds, the remainder of the duct is slender; the spermatheca is ovate. Interior of the vagina and free oviduct bear many folds. The free oviduct is roughly ½ larger than the base of the penis, expanding greatly at the junction with the spermathecal duct and narrowing again before the junction with the uterus. Description is based on two dissections.











Figures 18–24. *Pilsbryna nodopalma.* **18–20.** UF 294574, diameter 3.2 mm. **21.** UF 294574, diameter 3.2 mm; **22.** UF 24574. **23.** Camera lucida drawings of genitalia, UF 294575, maximum width 4.0 mm. **24.** UF 294575, horizontal field width 167 μm.

The central tooth of the radula is tricuspid; the mesocone is elongate (Figure 24). The ectocones are short, symmetric and diamond-shaped. The three lateral teeth are tall, slender and asymmetrically tricuspid. The endocones of the laterals are tall and flare away from the mesocone, while the ectocones are short and not as strongly differentiated. The peripheral margin of the mesocone of the laterals is concave above the ectocone. There are twelve unicuspid marginal teeth on each side, all with concave peripheral and convex proximal, margins. Based on the examination of two radulae.

Holotype: UF 304986, J. Slapcinsky and H. G. Lee, 9 Jun. 2001.

Paratypes: UF 286492, type locality, B. A. Brown, May 1989; UF 294574, UF 294575, type locality, J. Slapcinsky and H. G. Lee, 9 Jun. 2001; UF 294573, UF 294574, Betsy's Gap, State Road 209, 0.5 km SW of summit, 35°41.3′ N, 82°54.3′ W, 1150 meters elevation; UF 294571, UF 294571, J. Slapcinsky, 11 Mar. 2001, 29 May 2001; UF 292056, Harmon Den Road 1.4 km SW of Max Patch Road, 35°46.5′ N, 82°57.8′ W, 1000 meters elevation, J. Slapcinsky and H. G. Lee, 9 Jun. 2001; UF 292713, Madison County: State Road 63 at Friezeland Creek, 35°43.6′ N, 82°50.5′ W, 1000 meters elevation, J. Slapcinsky and H. G. Lee, 9 Jun. 2001; UF 294577, 0.3 km NE of junction of State Road 1175 and State Road 1182, 35°44.7′ N, 82°57.0′ W, 1170 meters elevation, J. Slapcinsky and H. G. Lee, 9 Jun. 2002; BC 1930, Tennessee, Greene County: Cherokee National Forest, Paint Creek Use Area, Hurricane Gap Road 3.2 km from Paint Creek, 35°57.9′ N, 82°50.5′ W, 640 meters elevation, B. Coles; UF 293022, Paint Creek near Forest Road 31, 1.3 km SW of fee station, 35°58.3′ N, 82°51.0′ W, 500 meters elevation, J. Slapcinsky, 1 Jun. 01; UF 293059, Paint Creek Road 5.3 km SW of fee station near junction with Forest Road 31, 35°57.3′ N, 82°53.4′ W, 420 meters elevation, J. Slapcinsky, 1 Jun. 01; BC 6763, Forest Road 3 by Paint Creek, B. Coles, 21 May 2002, 35°58.6′ N, 82°50.7′ W.

Type locality: USA, North Carolina, Haywood County, Carter Mountain Road at small stream 0.3 km SE of State Road 209, 35°40.7′ N, 82°54.4′ W, 1030 meters elevation.

Habitat and Distribution: *Pilsbryna nodopalma* is known from sites that extend for 50 km along the mountains on the North Carolina-Tennessee border, northwest of Asheville. Specimens have been found at 400–1100 m elevation usually on wooded, rocky hillsides in leaf-litter. Although, like other species of *Pilsbryna*, this species is found in moist leaf-litter, it is also found among leaves on relatively dry rock outcrops.

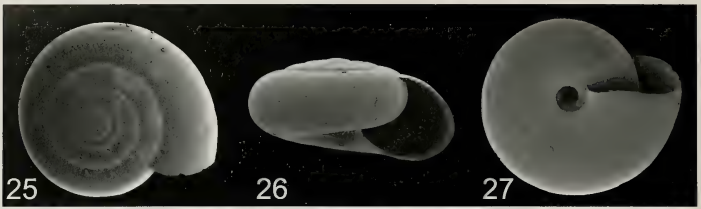
Etymology: Named for the dorsoventrally compressed apertural nodes that resemble the ends of oars (Latin, *noda* = knot and *palma* = palm or oar blade). For the purposes of the American Fisheries Society list of the common names of mollusks (Turgeon et al., 1988, 1998) and other administrative uses, the common name "oar tooth bud" is proposed.

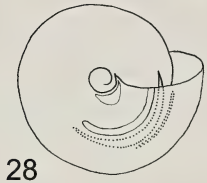
Remarks: Juveniles of *Pilsbryna nodopalma* are most likely to be confused with *P. vanattai*, the only other species with a series of palatal nodules. *Pilsbryna nodopalma* has nodules at the lower palatal position and the distal edge of the parietal lamella points toward these. In contrast, in *P. vanattai* the nodules are at midpalatal position and the distal edge of the parietal lamella points below these nodules. The nodules of *P. nodopalma* are dorsoventrally compressed, unlike the simple peg-shaped to elongate nodules of *P. vanattai*. Adults of *P. nodopalma* differ from all other species of *Pilsbryna* in having the whorls widest above mid-point rather than below. The penis, epiphallus and free oviduct are more robust than in other species of *Pilsbryna* except for *P. vanattai*. The endocones of the lateral teeth of *P. nodopalma* flare away from the mesocone, more so than any other species of *Pilsbryna*. A juvenile *Pilsbryna* specimen figured by Lee (1990) is this species.

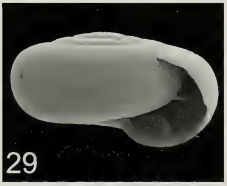
Pilsbryna quadrilamellata new species
Common name: four blade bud
(Figures 25–31, Table 1)

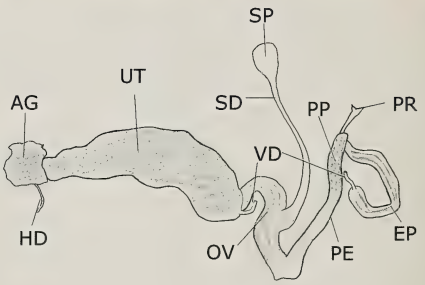
Diagnosis: A small to medium sized *Pilsbryna* with a shell of 2.8–3.2 mm diameter, 1.5–1.8 mm height, with 4.7–5.2 slowly expanding whorls. Shells of immature animals contain four lamellae, a crescent-shaped umbilical lamella and blade-shaped parietal, basal and sutural lamellae located within ⅓ whorl of the aperture. Lamellae are reduced in adult specimens; however traces of lamellae, especially the basal lamella are visible in the shells of many adults.

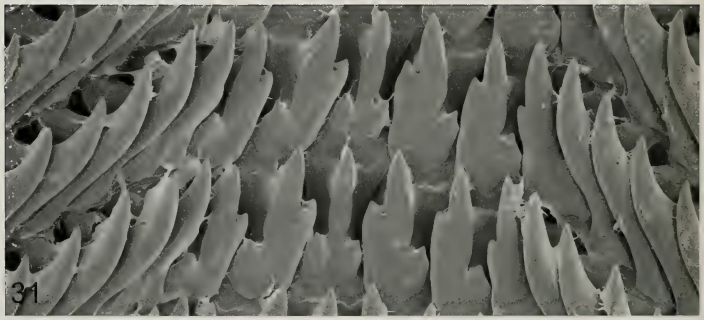
Description: Shell depressed-helicoid, umbilicate, glossy, and translucent with a sculpture of dense and irregularly spaced indented axial lines (Figures 25–27). Adult shells (Table 1) are about 2.8–3.4 mm (mean = 3.2, n = 10) in major diameter and 1.5–1.8 mm (mean = 1.7) in height with 4.7–5.2 (mean = 5.0) whorls. Shell height is 0.47–0.61 (mean = 0.52) of greater diameter. The whorls expand slowly and regularly; the lesser/greater diameter ratio of adult shells is 0.81–0.91 (mean = 0.87) the spire-width/greater diameter ratio 0.55–0.67 (mean = 0.61). The funnel-shaped umbilicus expands regularly; the umbilical width is 0.4–0.6 mm (mean = 0.5) and the ratio of umbilical width to greater diameter is 0.13–0.19 (mean = 0.17). The aperture of juvenile shells is evenly crescentic. In adults the sutural edge of the lip is flattened and the body whorl is widest basally. Shells of juveniles contain four lamellae at columellar, basal, sutural and parietal positions (Figures 28–29). The columellar lamella is short and crescent-shaped and is easily seen through the translucent base of the shell, although it often does not reach near enough to the aperture to be seen in apertural view. The basal lamella is thick, the distal edge broadly rounded. The sutural lamella is narrow, the distal edge evenly rounded and is











Figures 25–31. *Pilsbryna quadrilamellata*. **25–27.** UF 292445, diameter 3.4 mm. **28.** UF 292445, diameter 2.5. **29.** UF 292445, diameter 2.1 mm. **30.** Camera lucida drawings of genitalia, UF 292442, maximum width 5.8 mm. **31.** UF 292442, horizontal field width 150 μm.

most easily seen in an apical view through the translucent shell. The parietal lamella is thin and blade-shaped, tapering distally to a sharp edge. All four lamellae are reduced as individuals reach maturity; however some trace of lamellae, especially the basal lamella, remains in many adults.

The penis is relatively long and slender, apically papillate and basally smooth (Figure 30). The epiphallus is moderately long and slender, roughly the same diameter and length as the penis. The penial retractor muscle is inserted nearly apically on the penis. The epiphallus joins the penis subapically. The interior of the epiphallus bears strong internal folds. The spermathecal duct is long and slender and expands slightly at the junction with the free oviduct. The interior of the vagina, free oviduct and base of the spermathecal duct have weak folds. The free oviduct is about ⅓ larger than the base of the penis, and does not expand significantly at the junction with the base of the spermathecal duct. Two animals were dissected.

The central tooth of the radula is tricuspid; the mesocone is very slender and elongate (Figure 31). The ectocones are relatively short, a little more than ⅓ the total tooth height, symmetric and not significantly constricted basally. The three lateral teeth are tall, slender and asymmetrically tricuspid. The endocones of the laterals are tall, while the ectocones short, less than ⅓ the height of the entire tooth. Both ectocones and endocones flare strongly away from the mesocone. Each side of the radula has eighteen, tall, slender and unicuspid marginal teeth, with concave peripheral and convex proximal margins. Description is based on examination of two radulae.

Holotype: UF 304987, J. Slapcinsky and B. Coles, 31 May 2001.

Paratypes: All from type locality: UF 292442, UF 292445, J. Slapcinsky and B. Coles, 31 May 2001; BC 6760, B. Coles, 20 May 2002; UF 288172, UF 297415, J. Slapcinsky, 10 Jun. 2002; UF 299538, J. Slapcinsky, 10 Sep. 2002.

Type Locality: USA, Tennessee, Unicoi County, Unaka Springs, cold air slope along Unaka Springs Road, 3.2 km S of Banner Hill, 36°05.9′ N, 82°26.7′ W, 520 meters elevation.

Habitat and Distribution: All *Pilsbryna quadrilamellata* specimens were collected from leaf-litter within approximately 20 m of the base of a talus slope on a NE facing slope of the Nolichucky River. The riverbank supports hemlock forest with cove hardwoods on thin, rich soil overlaying sandstone talus, with pockets of deep leaf-litter. A steady stream of cold air emanates from the base of the talus slope throughout the spring, summer, and fall. Local residents visit the cold air slope during the summer months and part of the base of the slope has been cleared to provide a seating area.

Etymology: Named for the unique arrangement of four blade-like apertural barriers (Latin, *quattuor* = four and *lamella* = blade). For the purposes of the American Fisheries Society list of the common names of mollusks (Turgeon et al., 1988, 1998) and other administrative uses, the common name "four blade bud" is proposed.

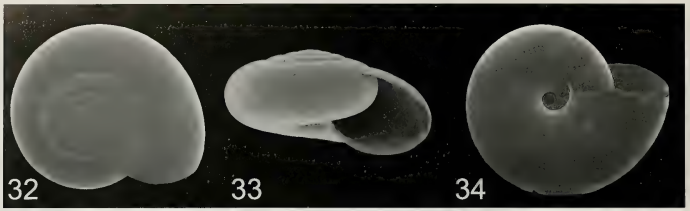
Remarks: The juvenile shell of *P. quadrilamellata* is unique in having a sutural lamella and a basal lamella that is long, thick and evenly rounded distally. It is most similar to *P. aurea,* both species having a crescent-shaped columellar lamella. The body whorl of *P. quadrilamellata* does not expand rapidly at maturity like most other *Pilsbryna* species. Adult *P. quadrilamellata* are unusual in having the sutural margin of the final third of the body whorl flattened. The penis and epiphallus of *P. quadrilamellata* are unusually delicate and elongate. The penis and epiphallus are uniform in width throughout, similar only to *P. nodopalma* and *P. vanattai.* The endocones of the lateral teeth of the radula flare strongly, similar only to those of *P. nodopalma* and the ectocones are relatively shorter than in any other species of *Pilsbryna.*

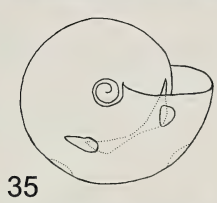
Pilsbryna vanattai (Walker and Pilsbry, 1902) new combination
Common name: honey glyph
(Figures 32–38, Table 1)

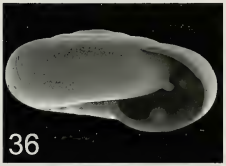
Vitrea vanattai Walker and Pilsbry, 1902: 432, pl. 23, figs. 4–6
Retinella (Glyphyalus) vanattai (Walker and Pilsbry, 1902). Baker, 1930: 205, pl. 10, figs. 9, 10; Pilsbry, 1946: 273–274, Fig 135; Burch 1962: 98, fig. 229.
Glyphyalinia vanattai (Walker and Pilsbry, 1902). Baker, 1962: 20; Hubricht, 1970: 13; Hubricht, 1985: 23, Map 212; Turgeon et al., 1988: 134; Turgeon et al., 1998: 147.

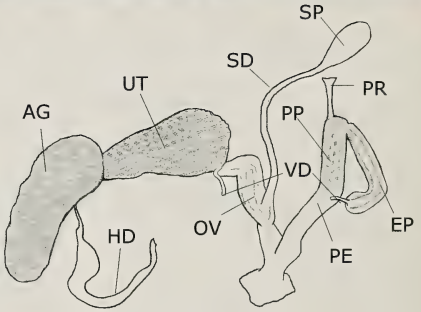
Diagnosis: A medium to large-sized, relatively depressed and loosely coiled *Pilsbryna* with a shell of 3.8–4.4 mm diameter and 1.9–2.2 mm height with 4.6–5.1 whorls. The body whorl of adults expands rapidly; the ratio of greater/lesser diameter of adult shells is 0.80–0.89. Juveniles have a sinuous parietal lamella and two spirally arranged series of one to three widely spaced paired basal and palatal nodules. The palatal lamella occupies a position lateral to and slightly above the parietal nodules.

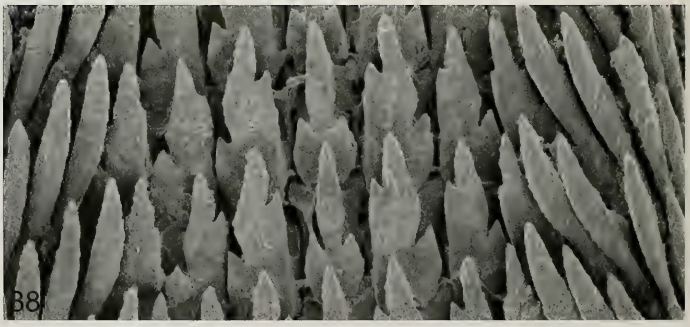
Description: Shell depressed-helicoid, umbilicate, and fragile, sculptured with irregular, impressed, axial lines (Figures 32–34). The sutures are shallow. Adult shells are relatively large (Table 1), 3.8–4.4 mm (mean = 4.0, n = 10) diameter, and 1.9–2.2 mm (mean = 2.0) height with 4.6–5.1 (mean = 4.8) whorls. The whorls expand slowly and regularly up to four whorls and then very rapidly, the ratio of lesser/greater diameter of adult shells is 0.80–0.89 (mean = 0.84). The rapid expansion of the body whorl results in low ratios for shell height/greater diameter of 0.48–0.56 (mean = 0.51) spire width/greater diameter 0.48–0.56 (mean 0.52) and umbilical width/greater diameter of 0.12–0.16 (mean = 0.14). The umbilicus is narrow until the final third of the











Figures 32–38. *Pilsbryna vanattai.* **32–34.** UF 279916, diameter 4.0 mm. **35–36.** UF 279916, diameter 2.0 mm. **37.** Camera lucida drawings of genitalia, UF 279917, maximum width 5.7 mm. **38.** UF 279917, horizontal field width 160 μm.

body whorl and then expands rapidly to 0.5–0.6 mm (mean = 0.5). Immature shells with fewer than 3.5 whorls have three lamellae: a sinuous parietal lamella and a series of paired basal and palatal nodules. When viewed from the aperture, the palatal lamella is situated lateral to and slightly above the parietal lamella. Two to three pairs of palatal and basal nodules can usually be seen through the base of the juvenile shell (Figures 35–36). These barriers are widely spaced, up to ⅓ whorl apart, and are usually completely resorbed in shells over 4 whorls. The undulating parietal lamella extends up to ⅔ of a whorl and is more prominent where it passes the paired basal and palatal lamellae.

The penis is papillate on its apical third and smooth basally (Figure 37). The penial retractor muscle inserts apically on the penis. The epiphallus joins the penis laterally at the apex, is short, only ⅔ the length of the penis, and robust, slightly narrower than the penis. The epiphallus is folded near mid-point, its interior has several strong, longitudinal folds and it is slightly swollen at the junction with the vas deferens. The interior of the vagina, free oviduct, and base of the spermathecal duct, bear many longitudinal folds. Three animals were dissected.

The central tooth of the radula is tall, slender and tricuspid (Figure 38). The mesocone is elongate, widest near mid-point and tapers apically and narrows basally. The ectocones are short, symmetrical and diamond-shaped. The three lateral teeth are tall, slender and asymmetrically tricuspid. The endocones of the laterals are tall and the ectocones short. The ectocones and endocones are well defined, but do not flare strongly away from the mesocone. The peripheral edges of the first two lateral teeth are concave. The third lateral tooth is notched above the ectocone. The twenty-two marginal teeth on each side of the radula are tall, slender and unicuspid, with concave peripheral edges and convex proximal edges. Two radulae were examined.

Lectotype: ANSP 83261a.

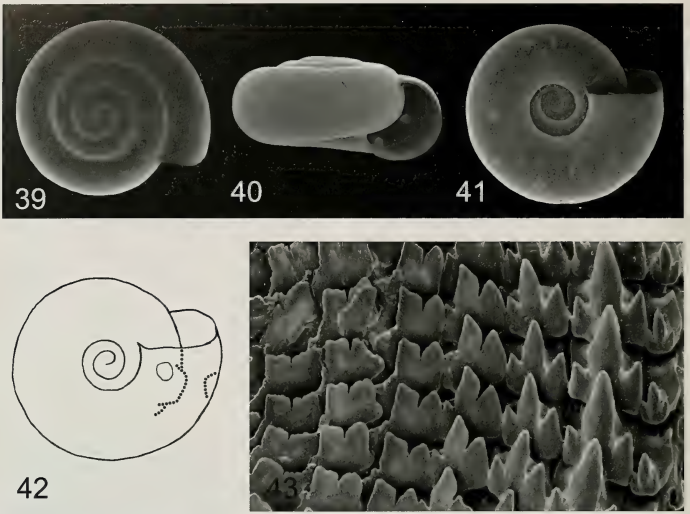
Paralectotype: ANSP 410030, from type locality, J.H. Ferriss, 1901.

Type Locality: USA, North Carolina, Yancey County, Mount Mitchell, J. H. Ferriss, 1901.

Other Material Examined: USA, North Carolina: Avery County, Cranberry, Baker (ANSP 158889). Buncombe County: Pisgah National Forest: State Road 197 ca. 9 km E of Barnardsville, 35°47.9′ N, 82°22.1′ W, 985 m elevation, J. Slapcinsky, 29 Apr 2000 (UF 279987); Walker Cove, Forest Road 74, ca. 7 km E of Dillingham, 35°45.7′ N, 82°21.6′ W, 1140 m elevation, J. Slapcinsky and R. Caldwell, 24 Apr 1998 (UF 279967), J. Slapcinsky and S. Florence, 27 Apr 2000 (UF 279916, UF 279917), J. Slapcinsky, 13 Mar 2001 (UF 287012), J. Slapcinsky, 1 Jun 2001 (UF 287010, UF 287011); Forest Road 74 at Perkins Road Trail, 35°44.9′ N, 82°21.4′ W, 1200 m elevation, J. Slapcinsky and S. Florence, 27 Apr 2000 (UF 279983, UF 279984); Forest Road 74, 0.5 km N of Laurel Gap Trail, 35°44.5′ N, 82°21.9′ W, 1200 m elevation, J. Slapcinsky and S. Florence, 27 Apr 2000 (UF 279986, NCSM P-4731); Douglas Falls Trail, 0.5 km S of Forest Road 74, 35°43.2′ N, 82°22.4′ W, 1350 m elevation, J. Slapcinsky and S. Florence, 27 Apr 2000 (UF 279988); Forest Road 63 ca. 8 km S of Dillingham, 35°42.6′ N, 82°23.7′ W, 1190 m elevation, J. Slapcinsky, 2 Jun 2001 (UF 287013); Bent Creek Experimental Forest, Forest Road 479, ca 1 km N of Blue Ridge Parkway, 35°27.7′ N, 82°39.7′ W, 860 m elevation, J. Slapcinsky, 2 Jun 2001 (UF 288621, UF 288622). Mitchell County: 1.9 km E of Spruce Pine, L. Hubricht, 4 Jun 1964 (FMNH 240499); Magnetic City, A. G. Wetherby, 1893 (ANSP 64609). Yancey County: near South Toe River, 7.2 km E of Mount Mitchell, 975 m elevation, L. Hubricht, 26 May 1962 (FMNH 240500); Black Mountains, Cat Tail Cove, J. H. Ferriss, 1901 (ANSP 84066). Tennessee: Carter County: Iron Mountain, Forest Road 4331 at Fall Branch, 36°9.1′ N, 82°10.7′ W, 1180 m elevation, J. Slapcinsky and B. Coles, 30 May 2001 (UF 292523); Roan Mountain, State Road 143 at Dave Miller Hollow Road, 36°10.3′ N, 82°6.1′ W, 840 m elevation, J. Slapcinsky and B. Coles, 30 May 2001 (UF 292505); Roan Mountain, behind picnic area W of Dave Miller Hollow Road, 36°10.3′ N, 82°5.9′ W, 850 m elevation, J. Slapcinsky and B. Coles, 30 May 2001 (UF 292470); 4.0 km S of Roan Mountain, L. Hubricht, 21 Sep 1967 (FMNH 240502); N outliers of Roan Mountain, Baker (ANSP 158887). Unicoi County, State Road 107, 0.5 km E of Red Fork Road, 36°9.2′ N, 82°14.9′ W, 880 m elevation, J. Slapcinsky and B. Coles, 31 May 2001 (UF 293083).

Habitat and Distribution: *Pilsbryna vanattai* has been found at sites between 800 and 1400 m elevation, ranging 120 km along the Blue Ridge of North Carolina and W into extreme eastern Tennessee (Pilsbry, 1946; Hubricht 1970, 1985). Specimens located in this survey were found at the soil leaf-litter interface on rich wet soils within a few meters of seeps, springs and small streams, often among stinging nettles, *Laportea canadensis* (Linnaeus, 1753), but also, less commonly, in deep leaf-litter at the base of rock outcrops.

Remarks: The juvenile shell of *Pilsbryna vanattai* differs from that of *P. nodopalma,* the only other species with palatal nodules, in having nodules that are not dorsoventrally compressed and that are located at mid-palatal rather than sub-palatal position. The body whorl of *P. vanattai* expands more rapidly than any other species of *Pilsbryna. P. vannattai* has the lowest ratios of lesser diameter/greater diameter, height/greater diameter, spire width/greater diameter, and umbilical width/greater diameter of any *Pilsbryna* species. The penises of *P. vanattai* and *P. nodopalma* are more robust than those of other species of *Pilsbryna.* The epiphallus of *P. vanattai* is relatively shorter than any other species, only about ⅔ the length of the penis. The ectocones and endocones of the lateral teeth of *P. vanattai* are well differentiated, unlike *P. aurea* and *P. castanea,* but do not



Figures 39–43. *Helicodiscus tridens.* **39–41.** UF 286491, diameter 1.6 mm. **42.** UF 286491, diameter 1.4 mm. **43.** UF 286491, horizontal field width 42 μm.

flare away from the mesocone, unlike *P. nodopalma* and *P. quadrilamellata.*

Walker and Pilsbry (1902) did not designate a holotype for *P. vanattai.* A single set of approximate measurements was given, but these could refer to either of the two adults of the three specimens mentioned in the description. Baker (1962) selected the specimen figured by Walker and Pilsbry (1902, figs. 4–6) to be the 'type', thereby designating the lectotype, and segregated it as 83261a. The remainder of the lot, the two paralectotypes, remained ANSP 83261. Later, the juvenile paralectotype was lost and the remaining paralectotype was recataloged (ANSP 410030).

Family Helicodiscidae
Genus *Helicodiscus* Morse, 1864

Helicodiscus tridens (Morrison, 1935)
Common name: crosstimbers coil
(Figures 39–43)

Pilsbryna tridens Morrison, 1935: 546, figs. 8–10; Pilsbry, 1946: 393, fig. 209; Burch, 1962: 106 fig. 25; Cheatum and Fullington, 1971: 9, fig. 12.

Helicodiscus tridens (Morrison, 1935). Hubricht, 1964: 28; Riedel, 1980: 52; Hubricht 1985: 20, fig. 182; Turgeon et al., 1988: 131; Turgeon et al., 1998: 148.

Holotype: USNM 359722, P. V. Roundy.

Type Locality: USA, Texas, Palo Pinto County, near Strawn.

Other Material Examined: USA, Oklahoma: Muskogee County, South Canadian River at Highway 2, 35°15.8′ N, 95°14.4′ W, 150 m elevation, B. Coles, 28 Nov 1998 (UF 286491); Haskell County, South Canadian River, Whitefield, L. Hubricht, 1935 (FMNH 239114); Texas, Colorado County, Colorado River at Columbus, H. F. Wickham, 8 Jan 1953 (ANSP 189563).

Habitat and Distribution: All previously known specimens of *Helicodiscus tridens* were collected from river drift or Pleistocene deposits from central Oklahoma to central Texas (Hubricht, 1985). Recent specimens of *H. tridens* including one with a dried animal were sifted from leaf-litter under willows, *Salix* sp.

Remarks: Comparisons of the species described in the genus *Pilsbryna* have highlighted the need to resolve the generic placement of *Helicodiscus tridens* (Morrison, 1935). *Helicodiscus tridens* was described as a *Pilsbryna* species based on similarities in the apertural barriers. Hubricht (1964) moved the species to the genus *Helicodiscus.* However, the basis for this change was not given, and the generic placement of the species has re-

44

Figure 44. Distribution of *Pilsbryna*: a = *Pilsbryna aurea*, c = *P. castanea*, n = *P. nodopalma*, q = *P. quadrilamellata*, v = *P. vanattai*. Map scale: 1 cm = 18 km.

mained unresolved. Characters other than those of the shell previously have not been available for study. Newly collected material, including a single dried animal, allows comparisons of both shell and radular morphology among *H. tridens* and species of *Pilsbryna* and *Helicodiscus*. Characters of the shell (Figures 39–42), including the nearly circular aperture, the small number of whorls (about 4 in adults), the flat apex and base, the impressed sutures, and the regularly expanding umbilicus, are not similar to species of *Pilsbryna*. However, they are consistent with *Helicodiscus, sensu lato*. The radula of *H. tridens* differs from *Pilsbryna* species. The row of tiny central teeth (Figure 43, far right), the much larger symmetric tricuspid lateral teeth and the short, broad, multicuspid marginal teeth are characteristic (Solem, 1975) of the helicodiscidae but are not found in *Pilsbryna*, thereby supporting Hubricht's (1964) placement of *H. tridens* in *Helicodiscus*.

DISCUSSION

When species of *Paravitrea* and *Helicodiscus* are separated from *Pilsbryna*, the geographic and microhabitat distribution of *Pilsbryna* is clarified. All known populations of *Pilsbryna* occur near springs, seeps and mountain streams in the southern Appalachian Mountains and nearby Cumberland Plateau (Figure 44). Within these areas, *Pilsbryna* species occupy moist microhabitats in damp, often deep, leaf-litter. It is likely that *Pilsbryna* species would be intolerant of habitat changes affecting

soil hydrology and leaf-litter cover. The narrow distribution and habitat specificity of species of *Pilsbryna* should make them species of special concern to land managers.

The terrestrial molluscan fauna of the southern Appalachian Mountains is by far the most diverse in eastern North America (Hubricht, 1985). Diversity notwithstanding, the region is still not well sampled, especially for small species with narrow habitat requirements. Recent collecting efforts in wet leaf-litter microhabitats uncovered not only the species reported here but also several others that require additional material to adequately describe. These results suggest there is a largely unreported radiation of *Pilsbryna* at springs and seeps throughout the southern Appalachian Mountains and Cumberland Plateau. Additional collecting in this region is necessary to determine the scope of this radiation.

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Staff of the Cherokee National Forest and Pisgah-Nantahala National Forest particularly Joe McGuiness and Sandy Florence generously shared their knowledge of the lands in their care. Peter Wyatt of the Tennessee Wildlife Resources Agency showed us the unusual cold-air talus slope at Unaka Springs. Harry G. Lee (Jacksonville, Florida) drew our attention to North Carolina populations of *Pilsbryna nodopalma,* donated specimens, and helped collect additional specimens. Ron Caldwell and Richard and Wanda Ott graciously hosted visits. We are particularly grateful to private land owners, Billie and John Brown, Walter McClain and the Davis family who allowed access to their lands. Jochen Gerber (FMNH) and Gary Rosenberg (ANSP) lent specimens and/or facilitated visits to collections in their care. Fred Thompson and Gustav Paulay (UF) commented on earlier drafts of this manuscript. Fieldwork was conducted with financial support from the Thomas L. McGinty Endowment Fund, University of Florida Foundation.

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The South American Mollusca of Johann Baptist Ritter von Spix and their publication by Johann Andreas Wagner

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ABSTRACT

Dr. Johann Baptist Ritter von Spix collected Mollusca in South America from 1817 to 1820. After his return to Europe he completed the plates, including their legends, and brief diagnoses for a monograph on the taxa he had collected, but died in 1826 before the main text was written. Dr. Johann Andreas Wagner was enlisted to complete the monograph, which he did, and it was published in 1827. In total, 64 gastropod and 20 bivalve taxa were illustrated. In developing the monograph for publication, Wagner altered Spix's concepts of many of the taxa, in some cases using his own name, not Spix's, as the author of the name. We discuss Wagner's rationale for making these changes. We discuss the appropriate citation of the authorship of the work, concluding that it should be cited as of Wagner alone. We also discuss the appropriate authorship of the species, concluding that in all cases in which Spix had provided a name on the plates authorship should be given as "Spix in Wagner". Wagner also created some new names, three of which are replacements for Spix's names, which are preoccupied, but the remaining ones are unnecessary replacement names for Spix's names (of which they are therefore junior objective synonyms) . Spix's type material is in the Zoologische Staatssammlung in Munich, although some of it is missing as a result of damage sustained during World War II.

INTRODUCTION

Johann Baptist Ritter von Spix was born in Höchstadt an der Aisch, near Bamberg, Bavaria, on February 9, 1781, as the son of a surgeon. [For additional biographic information see Fittkau (1983) and Huber and Huber (1993)]. He gained a doctorate in theology at the University of Bamberg but then changed his career to medicine, gaining a medical degree in 1806 from the University of Würzburg. He then practiced medicine for a short period before traveling to Paris in 1808 to meet Cuvier, Lamarck, and other well-known naturalists. On October 31, 1810, the Bavarian king, Maximilian I Joseph, made him adjunct (scientific assistant) to the curator of the zoological-zootomical collections of the Bavarian Academy of Sciences in Munich and, less than six months later, on April 24, 1811, following orders from the king, the Academy made him curator, and thus, director of these collections. During the period 1808–1811 Spix traveled not only in France but also in Italy and Switzerland. In 1811, he published his major work, *Geschichte und Beurtheilung aller Systeme in der Zoologie* [= History and evaluation of all systems in zoology] (xiv + 710 p., Achrag'sche Buchhandlung, Nürnberg). Spix greatly improved the old-fashioned arrangement of the natural history cabinet of the Bavarian Academy of Sciences and is regarded as the founder of the modern Bavarian zoological collections, now the Zoologische Staatssammlung München (ZSM).

In 1817, in the company of botanist Carl Friedrich Philipp von Martius (1794–1862) and a number of other naturalists, Spix embarked on a major expedition of exploration and natural history collecting to Brazil. They returned to Europe on December 10, 1820, with an enormous quantity of material that they had collected, which was deposited in the Bavarian Academy of Sciences where Spix was curator.

Based on that extensive material, Spix published numerous works, on monkeys and bats, turtles and frogs, lizards, and birds. Martius published on the plants. Sadly, only six years after his return from South America, Spix died, in Munich on May 15, 1826, apparently as a result of lingering illness contracted during the expedition. As a consequence, Spix's intended publications on fishes, insects, and mollusks remained unfinished and had to be completed by others.

Under the auspices of the editors (Franz von Paula von Schrank and Martius), the mollusk volume (*Testacea fluviatilia* . . .) was completed by Dr. Johann Andreas Wagner (March 21, 1797–December 17, 1861) and published in 1827. The primary aim of this paper is to clarify the authorship of the species described therein, following, when pertinent, the *International Code of Zoological Nomenclature* (ICZN, 1999), hereafter the *Code*, as

well as correct attribution of the work itself. In order to do this, it is necessary to discuss in detail the history of the production of the volume.

HISTORY OF THE *TESTACEA FLUVIATILIA*

The title page of the original issue of the mollusk work printed in Munich is shown in Figure 1. The title translates as follows:

> Freshwater mollusks that, while traveling through Brazil during the years 1817–1820 commanded by and under the auspices of Maximilian Joseph I, Most August King of Bavaria, were collected and taken care to be painted by Dr. J. B. von Spix, former Civilian Knight of the Royal Order of the Bavarian Crown, Ordinary Member of the Bavarian Academy of Sciences, curator of the collections of the Royal zoological, zootomical and ethnographical Museum. Arranged, described and illustrated with observations by Dr. J. A. Wagner
> Edited by Dr. F. von Paula von Schrank and Dr. C. F. P. von Martius
> Munich
> Publisher C. Wolf
> 1827

A later issue was printed in Leipzig, also in 1827. It differs slightly in a number of ways, as discussed below.

In total, 64 gastropod and 20 bivalve species were illustrated. The title (*Testacea fluviatilia*), however, does not reflect the contents correctly because, although the preface reads that the mollusks studied only live in fresh waters (*"quae nonnisi aquas dulces incolunt"*), 43 out of 64 gastropod species are land snails (e.g., genera *Bulimus, Strophocheilus, Helix, Achatina*). This suggests that perhaps at least the editors (who were not malacologists) were not fully aware of the contents of the book. If Spix himself had had the opportunity of publishing his work, then he may have titled it *"Testacea fluviatilia et terrestria"* or *"Testacea Brasiliensia"*; the latter perhaps being his intention, as suggested by the heading on page 1 of the descriptive text, above the title of the *Ampullaria* section. Wagner, of course, knew that many species were terrestrial, which suggests that he was not involved in deciding the title of the work nor in the writing of the preface.

The preface (*"Praefatio"*) (Figure 2) to the work explains some of its history. It is difficult to translate it because several terms and structures are not classical, with many embedded sentences and quotations. For example, the preface begins with *"Reliquerat"* [= had left behind], which has its object *"icones"* [= illustrations] 21 words later. This object, *"icones"*, has two modifying sentences connected by *"ac"* [= and]; the first runs from *"ad exemplaria"* to *"illustratas"* (14 words), while the second runs from *"reliquis"* to *"servituras"* (12 words). Within this second sentence, *"animalium collectorum"* is a genitive construction with a seven-word adverbial phrase in between. We have tried to make the following translation as close to the original as possible; however this has led to the use of somewhat awkward English in places. Also, we have placed some nouns in brackets since in Latin it was common to omit them and leave the reader to recover the meaning from the adjective. In addition, some explanatory material and some of the original Latin wording is also placed in brackets for clarity. The following is our translation of the *"Praefatio"*.

PREFACE.

Dr. Johann Baptist von Spix, formerly our colleague in the Royal Academy of Sciences, whose death, premature and calamitous for letters [i.e., science], we grieve, had left behind him illustrations of the animals with shells [*"Testaceorum"*] and the fishes, from the examples deposited by him in the Brazilian collections of the Academy [*"in Museo academico Brasiliano"*], drawn on stone [i.e., lithographs] and illustrated in colors, and had intended to use the [illustrations] to serve [creation of] the missing descriptions of the animals collected while traveling through the wide provinces of Brazil. These [illustrations] were handed to us by a brother of the now deceased man to be shared with the supporters of Spix's works. And there were not-weak arguments that impelled us to put hands to work; mainly the vividness and fidelity of the illustrations themselves, and the value of the depicted shells, most of which are now made known for the first time to those curious about nature; the rest [of the illustrations], even if [the species] have been described by other authors, will nonetheless be worth viewing because, as they were collected by Spix, these authors will themselves have future testimonial [to their work] by matching their [shells] with the illustrations of the indefatigable traveler.

Doubtless, descriptions, observations and other [notes], which could be useful to explain the illustrations, were lacking; but nature offers itself to the eyes. Moreover, being constrained by other issues and dedicated to other studies, we would have hardly had the necessary free time to accomplish the work: it seemed to us that this was a task for a man that measured up to him [i.e., Spix]. Conveniently, we happened to find out that Dr. J. A. Wagner had been engaged for several years in a large and important study of conchology, and was striving to publish a continuation of the works of Chemnitz, under the name of the Museum Conchyliologicum; the learned man did not refuse the commission that we requested of him, and got to work in order to complete [the present book].

What he achieved is evident from the work itself. He worked very hard in order that these mollusks, which only live in freshwater, should be included within the genera established by Lamarck and other recent authors, in the conviction that he had to do so in the interest of science because those [genera] that were given by Spix did not rely on a solid foundation, but rather seemed to be based on weak characters. Similarly, for the species, he reduced many to already known species, and carefully added all their synonyms. Even though by doing this the number of species that we consider new decreases, it is still the case that a large number of new [species] survives, which cannot be unpleasing to those interested in nature.

We hereby offer this posthumous work, trusting that it will enhance the memory of this man of natural sci-

TESTACEA FLUVIATILIA

QUAE

IN ITINERE PER BRASILIAM

ANNIS MDCCCXVII — MDCCCXX

JUSSU ET AUSPICIIS

MAXIMILIANI JOSEPHI I.

BAVARIAE REGIS AUGUSTISSIMI

SUSCEPTO

COLLEGIT ET PINGENDA CURAVIT

Dr. J. B. de SPIX,

Quondam Ordinis Regii Coronæ Bavaricæ Civilis Eques, Academiæ scientiarum Bavaricæ Socius Ordinarius, Musei Regii zoologici, zootomici et ethnographici Conservator rel.

DIGESSIT, DESCRIPSIT ET OBSERVATIONIBUS ILLUSTRAVIT

Dr. J. A. WAGNER

EDIDERUNT

Dr. F. a PAULA de SCHRANK et Dr. C. F. P. de MARTIUS.

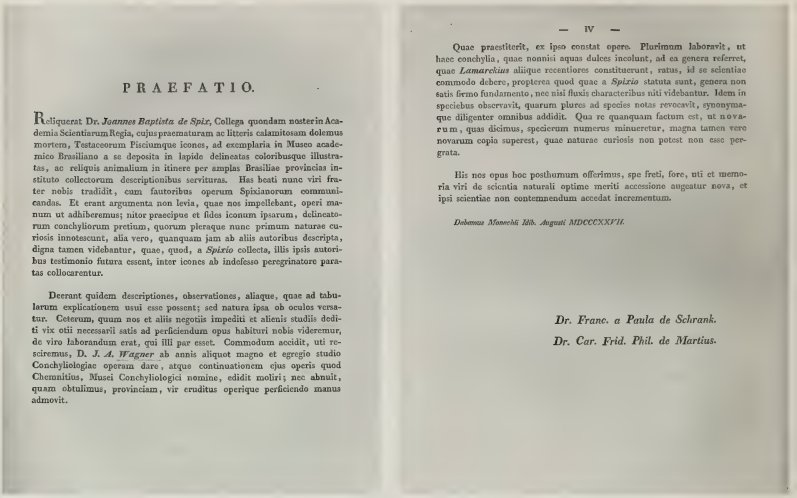
MONACHII,

TYPIS C. WOLF.

1827.

Bibliothek des Kgl. Zoolog. Museums

Figure 1. The title page of the Munich edition of the *"Testacea fluviatilia . . ."*.



PRAEFATIO.

Reliquerat Dr. *Joannes Baptista de Spix*, Collega quondam noster in Academia Scientiarum Regia, cujus praematuram ac litteris calamitosam dolemus mortem, Testacearum Piscisumque icones, ad exemplaria in Museo academico Brasiliano a se deposita in lapide delineatas coloribusque illustratas, ac reliquis animalium in itinere per amplas Brasiliae provincias instituto collectorum descriptionibus servituras. Has beati nunc viri frater nobis tradidit, cum fautoribus operum Spixianorum communicandas. Et erant argumenta non levia, quae nos impellebant, operi manum ut adhiberemus; nitor praecipue et fides iconum ipsarum, delineatorum conchyliorum pretium, quorum plerasque nunc primum naturae curiosis innotescunt, alia vero, quamquam jam ab aliis autoribus descripta, digna tamen videbantur, quae, quod, a *Spixio* collecta, illis ipsis autoribus testimonio futura essent, inter icones ab indefesso peregrinatore paratas collocarentur.

Deerant quidem descriptiones, observationes, aliaque, quae ad tabularum explicationem usui esse possent; sed natura ipsa ob oculos versatur. Ceterum, quum nos et aliis negotiis impediti et alienis studiisediti vix otii necessarii satis ad perficiendum opus habituri nobis videremur, de viro laborandum erat, qui illi par esset. Commodum accidit, uti rescireemus, D. *J. A. Wagner* ab annis aliquot magno et egregio studio Conchyliologiae operam dare, atque continuationem ejus operis quod Chemnitius, Musei Conchyliologici nomine, edidit moliri; nec abnuit, quam obtulimus, provinciam, vir eruditus operique perficiendo manus admovit.

— IV —

Quae praestiterit, ex ipso constat opere. Plurimum laboravit, ut hanc conchylia, quae nonnisi aquas dulces incolunt, ad ea genera referret, quae *Lamarckius* aliique recentiores constituerunt, ratus, id se scientiae commodo debere, propterea quod quae a *Spixio* statuta sunt, genera non satis firmo fundamento, nec nisi fluxis characteribus niti videbantur. Idem in speciebus observavit, quarum plures ad species notas revocavit, synonymaque diligenter omnibus addidit. Qua re quamquam factum est, ut novarum, quas dicimus, specierum numerus minueretur, magna tamen vero novarum copia superest, quae naturae curiosis non potest non esse peregrata.

His nos opus hoc posthumum offerimus, spe freti, fore, uti et memoria viri de scientia naturali optime meriti accessione augeatur nova, et ipsi scientiae non contemnendum accedat incrementum.

Dabamus Monachii Idib. Augusti MDCCCXXVII.

Dr. Franc. a Paula de Schrank.
Dr. Car. Frid. Phil. de Martius.

Figure 2. The "*Praefatio*" of the Munich edition of the "*Testacea fluviatilia* . . .".

ence of excellent merit through a new addition, and that it will be a non-negligible contribution to science itself.

Written in Munich, on August 13, 1827.

Dr. Franz von Paula von Schrank.
Dr. Carl Friedrich Philipp von Martius.

Thus, it is clear that Spix produced lithographs and that his brother passed them to the editors (Schrank and Martius), who in turn gave them to Wagner in order that he could produce the finished work, based upon Spix's illustrations. It is also clear that Spix provided names for his species.

Wagner was a systematist of the Blumenbach and Cuvier traditions (Martius, 1862). He is known to have avoided the creation of new genera and to have placed new species as far as possible in genera already established. His first published scientific work was in fact the description of the mollusks collected by Spix in Brazil. Gotthilf Heinrich von Schubert (1780–1860) and Wagner published, in 1829, the 12th volume of *Neues Systematisches Conchylien-Cabinet*, the famous German conchological series started by Friedrich Heinrich Wilhelm Martini (volumes 1–3, 1769–1774) and Johann Hieronymus Chemnitz (volumes 4–11, 1780–1788), as is alluded to in the preface (above), where reference is made to the "Museum Conchyliologicum" (which translates into English as "Conchological Museum" but was probably intended as the Latin translation of the German "Conchylien-Cabinet"). In 1831, Wagner published a handbook of the natural history of the animal Kingdom, focusing in particular on mammals.

Wagner obtained his Ph.D. in 1826 from the University of Erlangen, having previously spent two years (1814–1816) at the University of Würzburg. He then became a Privatdozent—a privately paid lecturer—in Erlangen, following a journey to Paris. On October 22, 1832, the Bavarian King awarded Wagner the position of adjunct (scientific assistant) to Schubert, his friend and Spix's successor as curator of the Munich zoological collection. It was apparently Schubert, following Spix's death in 1826, who arranged that Wagner be asked to publish Spix's material. The year 1832 is the earliest date we know for sure that Wagner was actually working in Munich. He became a member of the Royal Bavarian Academy of Science in 1835, and in 1849 was installed as the third curator of the zoological-zootomical cabinet. [For additional biographic information see Martius (1862)].

Wagner received, as the basic material for his study, the 29 plates that Spix had created, with Spix's names, and probably some notes and Latin diagnoses (see below). This corpus was wholly included in the book and Wagner used Spix's names, either confirming them or

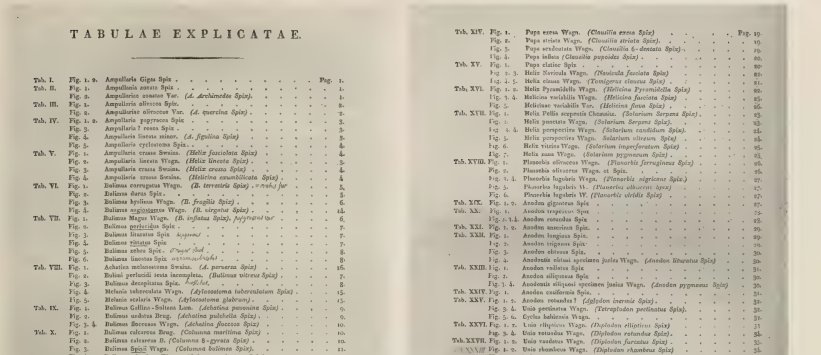

TABULAE EXPLICATAE.
Tab. I. Fig. 1. 9. Amphidromus Gigas Spix . . . . . Pag. 1.
Tab. II. Fig. 1. Amphidromus aureus Spix . . . . . 1.
Fig. 2. Amphidromus aureus Var. (A. dorbignyanus Spix). . . . . 1.
Tab. III. Fig. 1. Amphidromus olivaceus Spix. . . . . 2.
Fig. 2. Amphidromus olivaceus Var. (A. quercinus Spix) . . . . . 2.
Tab. IV. Fig. 1. 2. Amphidromus pygmaeus Spix . . . . . 3.
Fig. 3. Amphidromus ? roseus Spix . . . . . 3.
Fig. 4. Amphidromus lineatus minor. (A. fipalinus Spix) . . . . . 3.
Fig. 5. Amphidromus cyclostomus Spix. . . . . 4.
Tab. V. Fig. 1. Amphidromus crassus Swains. (Helix fasciolaria Spix) . . . . . 4.
Fig. 2. Amphidromus lineatus Wiegm. (Helix lineata Spix) . . . . . 3.
Fig. 3. Amphidromus crassus Swains. (Helix crassa Spix) . . . . . 4.
Fig. 4. Amphidromus crassus Swains. (Helix cinnabarinata Spix) . . . . . 4.
Tab. VI. Fig. 1. Bulimus corrugatus Wiegm. (B. terrestris Spix) . . . . . 5.
Fig. 2. Bulimus dorus Spix. . . . . 6.
Fig. 3. Bulimus hyalinus Wiegm. (B. fragilis Spix) . . . . . 6.
Fig. 4. Bulimus virginianus Wiegm. (B. virgineus Spix) . . . . . 14.
Tab. VII. Fig. 1. Bulimus Magus Wiegm. (B. infestus Spix, hypopurus Var. . . . . 6.
Fig. 2. Bulimus perdicinus Spix . . . . . 7.
Fig. 3. Bulimus lineatus Spix. Var. . . . . 7.
Fig. 4. Bulimus virtatus Spix . . . . . 7.
Fig. 5. Bulimus zebra Spix. Var. . . . . 8.
Fig. 6. Bulimus lineatus Spix. Var. . . . . 8.
Tab. VIII. Fig. 1. Achatina melanostoma Swains. (A. peruana Spix) . . . . . 16.
Fig. 2. Bulimi perlucidi testa incrustata. (Bulimus ustratus Spix) . . . . . 7.
Fig. 3. Bulimus decapitatus Spix. Var. . . . . 8.
Fig. 4. Helicis tuberculatae Wiegm. (Ampullaria tuberculatus Spix) . . . . . 15.
Fig. 5. Helicis scalaris Wiegm. (Ampullaria glabrata) . . . . . 15.
Tab. IX. Fig. 1. Bulimus Gallus-Soltani Lam. (Achatina punctata Spix) . . . . . 9.
Fig. 2. Bulimus undatus Brug. (Achatina pulchella Spix) . . . . . 9.
Fig. 3. 4. Bulimus Decorsus Wiegm. (Achatina flocculus Spix) . . . . . 10.
Tab. X. Fig. 1. Bulimus calcareus Brug. (Columna maritima Spix) . . . . . 10.
Fig. 2. Bulimus calcareus B. (Columna 8-gyrata Spix) . . . . . 10.
Fig. 3. Bulimus Spixii Wiegm. (Columna bulimus Spix). . . . . 11.
Fig. 4. Bulimus sulcatinus Wiegm. (Columna sulcatina Spix) . . . . . 11.
Fig. 5. Lymnaeus papyraceus Spix . . . . . 17.
Tab. XI. Fig. 1. Bulimus ovatus Brug. (Strophocheilus Hamadryas Spix) . . . . . 12.
Fig. 2. 3. Bulimus virgineus Brug. (Strophocheilus Alnicolus Spix) . . . . . 12.
Tab. XII. Fig. 1. 2. Bulimus notostomatus Swains. (Auris nucleatina Spix) . . . . . 13.
Fig. 3. Auricula signata. (Auris signata Spix) . . . . . 17.
Fig. 4. Auricula signata Var. (Auris ulvata Spix) . . . . . 13.
Tab. XIII. Fig. 1. 2. Auricula Largaris Lam. (Succinea auricula Spix) . . . . . 18.
Fig. 3. Bulimus angulatus Wiegm. (Succinea Pupa Spix) . . . . . 14.
Fig. 4. Bulimus notostomus Wiegm. (Succinea Cognata Spix) . . . . . 14.
Tab. XIV. Fig. 1. Pupa ovata Wiegm. (Clausilia ovata Spix) . . . . . Pag. 19.
Fig. 2. Pupa striata Wiegm. (Clausilia striata Spix). . . . . 19.
Fig. 3. Pupa sexdentata Wiegm. (Clausilia 6-dentata Spix) . . . . . 19.
Fig. 4. Pupa labiata (Clausilia papoidea Spix) . . . . . 60.
Tab. XV. Fig. 1. Pupa elatior Spix . . . . . 20.
Fig. 2. 3. Helix Succinea Wiegm. (Physicula fasciata Spix) . . . . . 20.
Fig. 4. 5. Helix ciuxa Wiegm. (Tornatina cinxata Spix) . . . . . 21.
Tab. XVI. Fig. 1. 2. Helix Pyramidella Wiegm. (Helicina Pyramidella Spix) . . . . . 22.
Fig. 3. 4. Helicina variabilis Wiegm. (Helicina fasciata Spix) . . . . . 23.
Fig. 5. Helicinae variabilis Var. (Helicina fenax Spix) . . . . . 23.
Tab. XVII. Fig. 1. Helix Pellis serpentis Chemnitz. (Solarium Serpens Spix) . . . . . 23.
Fig. 2. Helix punctata Wiegm. (Solarium Serpens Spix). . . . . 23.
Fig. 3. 4. Helix perspectiva Wiegm. (Solarium candidum Spix). . . . . 24.
Fig. 5. Helix perspectiva Var. (Solarium Serpens Spix) . . . . . 24.
Fig. 6. Helix vitrea Wiegm. (Solarium imperforatum Spix) . . . . . 25.
Fig. 7. Helix zona Wiegm. (Solarium zygonotum Spix) . . . . . 25.
Tab. XVIII. Fig. 1. Planorbis olivaceus Wiegm. (Planorbis ferrugineus Spix) . . . . . 26.
Fig. 2. Planorbis olivaceus Var. et Spix. . . . . 26.
Fig. 3. 4. Planorbis lugubris Wiegm. (Planorbis nigricans Spix.) . . . . . 27.
Fig. 5. Planorbis lugubris Var. (Planorbis obscurus Spix) . . . . . 27.
Fig. 6. Planorbis lugubris Var. (Planorbis viridis Spix) . . . . . 27.
Tab. XIX. Fig. 1. 2. Amnicus glaucus Spix . . . . . 27.
Tab. XX. Fig. 1. Amnicus tropicus Spix . . . . . 72.
Fig. 2. 3. Amnicus cornucus Spix . . . . . 28.
Tab. XXI. Fig. 1. 2. Amnicus anceinus Spix. . . . . 29.
Fig. 3. Amnicus longaeus Spix. . . . . 29.
Fig. 4. Amnicus trigonus Spix . . . . . 29.
Fig. 5. Amnicus olivaceus Spix. . . . . 30.
Fig. 6. Amnicinia viridis specimen Junius Wiegm. (Amnicus Riisaetus Spix) . . . . . 30.
Tab. XXII. Fig. 1. Amnicus vallatus Spix . . . . . 31.
Fig. 2. Amnicus nitidissimus Spix . . . . . 30.
Fig. 3. 4. Amnicinia nitidissimi specimen Junius Wiegm. (Amnicus pygmaeus Spix) . . . . . 30.
Tab. XXIII. Fig. 1. Amnicus emiliensis Spix. . . . . 31.
Tab. XXV. Fig. 1. 2. Amnicus rotundus ? (Affinis inermis Spix) . . . . . 30.
Fig. 3. 4. Unio pernicetus Wiegm. (Tetrapodon perlinatus Spix). . . . . 32.
Fig. 5. 6. Cyclas baltaicus Wiegm. . . . . 32.
Tab. XXVI. Fig. 1. 2. Unio ellipticus Wiegm. (Diplodon ellipticus Spix) . . . . . 33.
Fig. 3. 4. Unio rotundus Wiegm. (Diplodon rotundus Spix). . . . . 34.
Tab. XXVII. Fig. 1. 2. Unio vaudatus Wiegm. (Diplodon furcatus Spix) . . . . . 34.
Fig. 3. 4. Unio rhombeus Wiegm. (Diplodon rhombeus Spix) . . . . . 34.
Fig. 5. 6. Unio regnus Wiegm. (Triplodon regnus Spix) . . . . . 35.

Figure 3. The *"Tabulae explicatae"* of the Munich edition of the *"Testacea fluviatilia . . ."*.

reducing them to synonymy. Wagner also included two pages of *"Tabulae explicatae"* (Figure 3), essentially an index that listed all the names in the sequence in which they appeared on Spix's plates, with reference to the text page on which Wagner gave his own opinions regarding what he had interpreted about each species.

AUTHORSHIP OF THE WORK

Prior to Spix's death, he had produced plates, with names, illustrating the species. Following his death, the editors enlisted Wagner to provide descriptions of the species, which he did. The completed work was published in 1827. In the past, some authors (e.g., Ihering, 1890; Haas, 1969) have considered Spix as sole author of the work, perhaps because he provided the plates, legends, and probably a short diagnosis for each species (see below) that are the foundation of the work, which Wagner simply prepared for publication, that is, as a scientific editor of Spix's work. Others, however, most likely because Spix did not provide the text of the descriptions but only the names and illustrations (and probably the short diagnoses), have attributed authorship of the work either to Wagner alone (because he was the author of the descriptions) or to Spix and Wagner (as suggested for example by Glaubrecht (1996: 488)), following the convention that a name and illustration alone (Spix's contribution) did not satisfy the criteria of nomenclatural availability. However, the *Code* (Article 12.2.7) states that a name associated with an illustration, published before 1931, is sufficient to establish availability. Thus, Spix's contribution to the work is sufficient to validate his authorship of the names associated with the illustrations on the plates, even in the absence of Wagner's descriptions, which also, however, standing alone, would be sufficient to validate the names. Additional reasons for attributing most of the names to Spix are discussed below.

Given Spix's contribution, that it is explicitly acknowledged in the preface, that his name is clearly part of the title page (in fact appearing first), and that there is no evidence that the plates were published separately from the text, authorship of the work should arguably be attributed to both Spix and Wagner, and in that order because that is the order in which they appear on the title page. Based on this argument, that is, that the work is neither Wagner's nor Spix's work alone, but their mixed contributions, authorship of the work as of Spix and Wagner could be justified, as was accepted by Fechter (1983b).

A similar argument was used by Kottelat (1988) in deciding that authorship of the work *"Selecta genera et species piscium quos in itinere per Brasiliam . . . collegit et pingendos curavit Dr J.B. de Spix"* on the fishes collected by Spix but published (in two fascicles: June 1829, January 1831) by Louis Agassiz (1807–1873) should be

attributed to Spix and Agassiz. This volume, the first monograph on Brazilian fishes, also contains descriptions of numerous new species and genera. While the plates of this fish volume were prepared at least in part under Spix's supervision, the text was written by Agassiz. However, Kottelat (1988: 73) argued, based on article 50(a) of the *Code* (3rd edition, 1985) and the fact that Spix was not author of both the names and the conditions making them available, that for nomenclatural purposes Agassiz is the sole author of the names. It appears that Agassiz wrote the whole of the text, and whatever Spix wrote, can only have been rough notes, although he provided the species names for the plates. According to Kottelat (1988: 73), most plates of the first fascicle were engraved and colored before Spix's death and bear the names Spix intended to give them. As we have seen above, however, a name associated with an illustration, published before 1931, is indeed sufficient to establish availability (and this was the case also in the 3rd edition of the *Code*). Thus, in this regard, Kottelat's interpretation of the *Code* was incorrect. As Wagner did in the case of the mollusks, in several cases Agassiz did not follow Spix's names on the plates of the first fascicle (regarding the names as inappropriate or in a "barbarian language" or the fishes as misidentified) and therefore introduced other names in the text. In contrast, the plates of the second fascicle bear names consistent with the text, undoubtedly given by Agassiz. Nevertheless, Kottelat decided, following Recommendation 51B of the *Code* (3rd edition), that the species names should be cited as "Agassiz in Spix and Agassiz", arguing that this seemed desirable to him "for bibliographic purposes".

Notwithstanding this entire argument, authorship of the work is not regulated by the *Code* and the most appropriate attribution of the work remains open for discussion. Spix's name forms part of the title, since the relative pronoun *"quae"* [= "that"] on the second line of the title page (Figure 1) opens a subordinate sentence with a subject ("Dr. J. B. de Spix") that requires one or more verbs (*"collegit et pingenda curavit"*) to give meaning to the sentence. But conversely, Wagner's and the editors' contributions are not part of the title—Wagner "arranged, described and illustrated with observations" (see above) the work of Spix. The book does not contain only Spix's concepts, nor did Wagner communicate with him to clarify the reasons why Spix considered some of the shells as belonging to new species. Indeed there is no evidence that they ever met. In fact, Spix's views were contradicted several times in the text. So, the book is not a unity (i.e., a Spix-and-Wagner production) but an earlier work by Spix, critiqued and modified by Wagner. Therefore we consider that Wagner, being responsible for presenting the material following his own criteria, and deciding the fate of the work after Spix's death, is to be credited with the final product, as the only author of a book into which Spix's contribution has been incorporated.

We therefore consider it most appropriate to treat Wagner as the sole author of the book, which should then be cited as

> WAGNER, J.A. 1827. Testacea fluviatilia quae in itinere per Brasiliam annis MDCCCXVII–MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae regis augustissimi suscepto collegit et pingenda curavit Dr. J. B. de Spix, quondam ordinis regii coronæ Bavaricæ civilis eques, academiæ scientarum Bavaricæ socius ordinarius, musei regii zoologici, zootomici et ethnographici conservator rel. C. Wolf, Monachii [= Munich]. iv + [ii] + 36 pp., 29 pls.

Another issue of the work was also published in Leipzig, but we consider this to have been published subsequent to the Munich edition, as discussed below.

AUTHORSHIP OF THE SPECIES

The following discussion relates to the Munich issue, as the Leipzig issue, published after the Munich issue (see below), has no bearing on nomenclature.

Spix consistently provided binomina in the figure legends for the new species he illustrated in the plates. He thereby accomplished the minimum pre-1931 conditions of availability for those names (*Code,* Articles 11 and 12), except for publication. It seems that he also provided two to three line diagnoses (see below). Arguably, because Wagner provided the longer descriptions (for most species), he also could be construed as an author, since the plates, diagnoses, and longer descriptions were published simultaneously. So, arguably, authorship could undoubtedly be considered as "Spix and Wagner" for all those species originally named by Spix.

Of course, Spix failed to publish his new species independently, but the act of being published by another person (Wagner) does not necessarily deprive Spix of nomenclatural authorship because, "if it is clear from the contents that some person other than the author of the work is alone responsible both for the name or act and for satisfying the criteria of availability *other than actual publication* [our italics], then that other person is the author of the name or act" (*Code,* Article 50.1.1). Wagner was careful to keep authorships recognizable by identifying them in the text and in the index [the *"Tabulae explicatae"*]. So, the illustrations, created by the deceased Spix, with associated names that were attributed to Spix, were published as a corpus together with an index in which each plate was listed in Spix's sequence. Thus, the names attributed to Spix in the work should indeed be attributed to Spix alone and not to Spix and Wagner. This has been the conclusion reached by earlier authors (e.g., Ihering, 1890; Morrison, 1954; Haas, 1969; Fechter, 1983a, b).

Furthermore, regarding precedence of Spix and Wagner's names and nomenclatural acts, the *Code* (Recommendation 24B) states that "Zoologists acting as First Revisers to determine the precedence of identical names published in the same or different works, and on the same day, are advised to follow attributions by authors concerned if these are known". And the *Code* (Article

50.6) states that "When two or more identical names for the same taxonomic taxon are published on the same date, by different authors in the same or different works, their precedence (and hence the authorship of the name) is determined by the application of Article 24". Therefore, because Wagner attributed the names to Spix, the latter's names take precedence, even though published simultaneously with the former's names. The following example is illustrative. Wagner considered *Ampullaria archimedes* Spix a synonym of *A. zonata* "Wagner" on the basis of Spix's figure alone; i.e., "*. . . quae mihi tantum ex hac figura cognita est*" [= "*. . .* which I only know from this figure"]. Therefore, *A. archimedes* cannot be co-authored by Wagner, because he did not consider it a valid species. The species has to be credited to Spix; thus, Wagner's act was to create a subjective synonym.

Both authors worked independently and did not share their taxonomic concepts, a further reason for authorship of the taxa not being Spix and Wagner, but Spix (or Wagner in a few cases) alone. Table 1 lists all the names of both authors, with their correct authorship and status.

Wagner's rationale for attributing authorship does not follow current rules of nomenclature. He accepted as of Spix only those species that he considered valid and correctly combined with a generic name (25 of the 84 species illustrated by Spix). In modern terms, citation of these species should be either as of Spix alone (*Code,* Article 50.1.1) or as of Spix in Wagner (*Code,* Recommendation 51E). On the basis of the following discussion, we consider that the names should be cited as of Spix in Wagner, with a small number of exceptions.

In the 13 cases in which Wagner transferred one of Spix's species to another genus he presented himself as the author (*Ampullaria lineata* Wagner for *Helix lineata* Spix, *Pupa exesa* Wagner for *Clausilia exesa* Spix, *Helix clausa* Wagner for *Tomigerus clausus* Spix, etc.). This was common practice for several decades in the late 1700s and early 1800s. He did not question the validity of such species, but simply re-assigned them to genera established by Lamarck and other authors (as explained in the Preface, above). This action is now treated as establishing a new combination, so a reference such as "Bulimus sylvaticus Wagn. *(Columna sylvatica Spix)*" [in the "*Tabulae explicatae*"] is now treated as *Bulimus sylvaticus* (Spix) or *Bulimus sylvaticus* (Spix) Wagner (*Code,* Recommendation 51G), although the latter practice has rarely, if ever, been used in mollusks.

Wagner changed three names because those given by Spix were preoccupied (i.e., *Bulimus hyalinus* Wagner for *B. fragilis* Spix, non Lamarck; *Bulimus magus* Wagner for *B. inflatus* Spix, non Lamarck; *Helicina variabilis* Wagner for *H. fasciata* Spix, non Lamarck). In these cases, Spix's names are junior primary homonyms and therefore invalid.

Wagner also changed other names, but for no explicit reason (e.g., *Melania scalaris* Wagner for *Aylacostoma glabrum* Spix; *Unio caudatus* Wagner for *Diplodon furcatus* Spix). In these cases, Spix's names are valid, while Wagner's are unnecessary replacement names and thus junior objective synonyms (*Code,* Article 72.7).

Finally, in some cases Wagner added his name following what appear to be replacement names for some of Spix's binomina; however, the new names were not binominal and therefore not available. For example, *Anodon lituratus* Spix became "Anodontis obtusi specimen junius Wagn." [= "a young specimen of *Anodon obtusus* Wagner", although he attributed *Anodon obtusus* to Spix]. Similarly, and although Wagner did not add his name in this case, *Ampullaria figulina* Spix became "Ampullaria lineata minor" [= a smaller *Ampullaria lineata*]. In this instance "minor" is not to be considered a subspecific name forming part of a valid trinomen, but as a purely descriptive term. We conclude from these instances that Wagner aimed not to claim authorship of the species but to establish subjective synonymy.

Again, on the basis of all this evidence, the names are to be cited as of "Spix in Wagner", except in the case of the three invalid, preoccupied names of Spix, the replacements for which should be cited as of Wagner alone. The remainder of Wagner's names are unnecessary replacement names.

RELATIONSHIP OF THE TEXT TO THE PLATES

Most species are described twice. The first text, in a larger font, is a two to three line diagnosis mostly based on shape and colors, as are visible in Spix's figures. The second text, in a smaller font, is a more detailed description that also includes some measurements and information that can only be accurately assessed on actual shells (e.g., whorl number). An example is given in Figure 4. While it is possible that the first two-line text for each species is a description by Wagner of Spix's figure, and that the second text was written after comparing the plate with additional materials, we have no compelling evidence that this is the case. Rather, we believe that the short first text is attributable to Spix and only the longer second text to Wagner, for the following reasons.

The customary practice among conchologists at the time when describing new species was either to write all the text in Latin, i.e., a single description sometimes followed by comments (e.g., many papers in the *Zeitschrift für Malakozoologie* by Philippi, Pfeiffer, etc., Pfeiffer's *Monographia Heliceorum Viventium*), or to give a short Latin diagnosis, followed by additional descriptions and comments in a vernacular language (e.g., the *Voyage* of d'Orbigny, contributions to the *Systematisches Conchylien-Cabinet von Martini und Chemnitz* by Philippi, Küster, etc., Reeve's *Conchologia Iconica*). Neither of these patterns is followed. When Wagner shared Spix's concept and name for the species, then the two texts are arranged directly one after the other (e.g., *Ampullaria gigas, A. papyracea, A. rosea*). When, for some reason, Wagner changed the original name, usually because of a genus change (e.g., *Melania tuberculata* Wagner for *Aylacostoma tuberculatum* Spix), or to give a replacement name (e.g., *Pupa inflata* Wagner for *Clausilia pupoides*

Table 1. The names of Spix and Wagner listed in the order of Spix's plates and as they appear in the "*Tabulae explicatae*", with explanations of their treatment by Wagner if different from their treatment by Spix, and additional comments, as appropriate. In the "*Tabulae explicatae*" Wagner's treatment of the names appears in plain Roman type, with Spix's names in parentheses and italic type on the same line, if Wagner's treatment of them differed. All their new names are nomenclaturally available. Note that there are 29 printed plates, but that the *Tabulae explicatae* only number 27; the final two lines of the *Tabulae explicatae* lack the plate numbers, though the plates themselves have the correct legends: "Tab. XXVIII" and "Tab. XXIX".

Names as listed in the "*Tabulae explicatae*"	Plate and figure numbers	Names as they appear on the plates	Treatment by Wagner if different from that by Spix, with additional comments in square brackets
GASTROPODA			
Ampullaria Gigas Spix	Pl. I, figs. 1, 2	AMPULLARIA Gigas.	
Ampullaria zonata Spix	Pl. II, fig. 1	AMPULLARIA 1. zonata. 2. Archimedes.	[Listed as *Ampullaria zonata* Spix in the *Tabulae explicatae* but *Ampullaria zonata* Wagner in the text.]
Ampullaria Archimedes Spix	Pl. II, fig. 2	[see *Ampullaria zonata*]	Smaller variety of *A. zonata* Spix.
Ampullaria olivacea Spix	Pl. III, fig. 1	AMPULLARIA 1. olivacea. 2. quercina.	*A. guyanensis* Lamarck, 1822, given as a synonym but Spix's name retained as valid. Compared to *A. rugosa* Lamarck, 1801, *A. globosa* Swainson, 1823, and *A. leucostoma* Swainson, 1823. [Junion primary homonym of *Ampullaria olivacea* Lamarck, 1816.]
Ampullaria quercina Spix	Pl. III, fig. 2	[see *Ampullaria olivacea*]	Smaller variety of . *olivacea* Spix.
Ampullaria papyracea Spix	Pl. IV, figs. 1, 2	AMPULLARIA 1. 2. papyracea. 3. rosea. 4. figulina. 5. Cyclostoma.	
Ampullaria ? rosea Spix	Pl. IV, fig. 3	[see *Ampullaria papyracea*]	Valid species, although its identity as an *Ampullaria* doubted; considered a terrestrial snail in the genus *Bulimus*.
Ampullaria figulina Spix	Pl. IV, fig. 4	[see *Ampullaria papyracea*]	Smaller, yellowish variety of *Ampullaria lineata* (Spix).
Ampullaria cyclostoma Spix	Pl. IV, fig. 5	[see *Ampullaria papyracea*]	Extreme affinity to *Ampullaria effusa* (Müller, 1774) Swainson, 1823 [= *Nerita effusa* Müller, 1774] noted.
Helix fasciolata Spix	Pl. V, fig. 1	HELIX 1. fasciolata. 2. lineata. 3. crass. 4. HELICINA exumbilicata.	Variety of *Ampullaria crassa* Swainson, 1823, with a narrow umbilicus.
Helix lineata Spix	Pl. V, fig. 2	[see *Helix fasciolata*]	Placed in *Ampullaria* as *A. lineata* "Wagn." [= (Spix)]. *A. fasciata* Swainson, 1822, given as a synonym but Spix's name retained as valid. [*A. fasciata* Swainson, 1822, is a misidentification of *A. fasciata* Lamarck, 1816 (Cowie and Thiengo, 2003).] Compared to *A. reflexa* Swainson, 1823. [Junior primary homonym of *Helix lineata* Renier, 1804, and *Helix lineata* Say, 1817.]
Helix crassa Spix	Pl. V, fig. 3	[see *Helix fasciolata*]	Not a new name; = *Ampullaria crassa* Swainson, 1823.
Helicina exumbilicata Spix	Pl. V, fig. 4	[see *Helix fasciolata*]	Variety of *Ampullaria crassa* Swainson, 1823, lacking an umbilicus.
Bulimus terrestris Spix	Pl. VI, fig. 1	BULIMUS 1. terrestris. 2. durus. 3. fragilis. 4. virgatus.	[see *Bulimus corrugatus*, below]
Bulimus corrugatus Wagner	Pl. VI, fig. 1	[see *Bulimus terrestris*]	*Bulimus terrestris* Spix synonymized with *B. corrugatus* "Wagner" and considered to be but a juvenile of *Bulimus ovatus* (Müller, 1774) [= *Helix ovata* Müller, 1774], although *B. corrugatus* "Wagner" retained as the valid name. [Not a new name; = *Bulimus corrugatus* Bruguière, 1792.]
Bulimus durus Spix	Pl. VI, fig. 2	[see *Bulimus terrestris*]	
Bulimus fragilis Spix	Pl. VI, fig. 3	[see *Bulimus terrestris*]	Junior secondary homonym of *Bulimus fragilis* (Montagu, 1803) Lamarck, 1822 [= *Helix fragilis* Montagu, 1803].
Bulimus hyalinus Wagner	Pl. VI, fig. 3	[see *Bulimus terrestris*]	New replacement name for *Bulimus fragilis* Spix, non *Bulimus fragilis* (Montagu, 1803) Lamarck, 1822.

Table 1. Continued.

Names as listed in the *"Tabulae explicatae"*	Plate and figure numbers	Names as they appear on the plates	Treatment by Wagner if different from that by Spix, with additional comments in square brackets
Bulimus virgatus Spix	Pl. VI, fig. 4	[see *Bulimus terrestris*]	Incomplete shell of *Bulimus angiostomus* Wagner [= *Stenostoma capueira* Spix].
Bulimus angiostomus Wagner	Pl. VI, fig. 4	[see *Bulimus terrestris*]	[see additional listing, below]
Bulimus inflatus Spix	Pl. VII, fig. 1	BULIMUS 1. inflatus. 2. perlucidus. 3. lituratus. 4. vittatus. 5. Zebra. 6. lineatus.	Junior primary homonym of *Bulimus inflatus* Olivier, 1801, and *Bulimus inflatus* Lamarck, 1822.
Bulimus Magus Wagner	Pl. VII, fig. 1	[see *Bulimus inflatus*]	New replacement name for *Bulimus inflatus* Spix, non Olivier, non Lamarck.
Bulimus perlucidus Spix	Pl. VII, fig. 2	[see *Bulimus inflatus*]	
Bulimus lituratus Spix	Pl. VII, fig. 3	[see *Bulimus inflatus*]	*Helix lita* ["Freycinet, Voyage autour du monde"; = *Helix lita* Férussac in Quoy and Gaimard] given as a synonym but Spix's name retained as valid.
Bulimus vittatus Spix	Pl. VII, fig. 4	[see *Bulimus inflatus*]	
Bulimus zebra Spix	Pl. VII, fig. 5	[see *Bulimus inflatus*]	Treated as a valid species. Also mentioned a larger variety with a basal, dark color band. [Primary junior homonym of *Bulimus zebra* Olivier, 1801, and *Bulimus zebra* Perry, 1810. Perhaps not intended by Spix as a new name, but a misidentification of *Buccinum zebra* Müller, 1774].
Bulimus lineatus Spix	Pl. VII, fig. 6	[see *Bulimus inflatus*]	Exreme similarity to *"Bulimus radiatus"* noted. [Junior primary homonym of *Bulimus lineatus* Draparnaud, 1801. ? = *Bulimus radiatus* de Blainville, 1825—apparently the only *Bulimus radiatus* described.]
Achatina perversa Spix	Pl. VIII, fig. 1	1. ACHATINA perversa. 2. BULIMUS vitreus. 3. BULIMUS decapitatus. 4. AYLACOSTOMA tuberculatum. 5. glabrum.	Synonym of *Achatina melanostoma* Swainson. Dextral and sinistral shells of this species mentioned as deposited in the Munich Museum. [Not a new name; = *Achatina perversa* Swainson, 1821 (originally spelled *"Achatinia"* by Swainson). The original name of *"Achatina melanostoma* Swainson" is *melastoma.* Even if *melanostoma* were preferable from a scholarly perspective, a poor latinization is not to be corrected (*Code,* Article 32.5.1). Because Wagner cited the original and the changed name, and used the latter as valid, the change is considered demonstrably intentional (*Code,* Article 33.2.1). Wagner's nomenclatural act being an unjustified emendation, *Achatina melanostoma* Wagner, 1827, is a junior objective synonym of *Achatina melastoma* Swainson, 1823.]
Bulimus vitreus Spix	Pl. VIII, fig. 2	[see *Achatina perversa*]	Synonym (an incomplete shell) of *Bulimus perlucidus* Spix.
Bulimus decapitatus Spix	Pl. VIII, fig. 3	[see *Achatina perversa*]	Extreme similarity to *Bulimus decollatus* (Linnaeus, 1758) Bruguière, 1789 [= *Helix decollata* Linnaeus, 1758] noted.
Aylacostoma tuberculatum Spix	Pl. VIII, fig. 4	[see *Achatina perversa*]	Placed in *Melania* as *Melania tuberculata* "Wagn." [= (Spix)]; compared to *Melania truncata* Lamarck, 1822.
Aylacostoma glabrum Spix	Pl. VIII, fig. 5	[see *Achatina perversa*]	Replaced by *Melania scalaris* Wagner.
Melania scalaris Wagner	Pl. VIII, fig. 5	[see *Achatina perversa*]	[Unnecessary replacement name for *Aylacostoma glabrum* Spix; junior objective synonym of *A. glabrum* Spix.]
Achatina pavonina Spix	Pl. IX, fig. 1	ACHATINA 1. pavonina. 2. pulchella. 3. 4. floccosa.	Not mentioned in the text; synonym of *Bulimus gallinasultana* Lamarck, 1822, in the *"Tabulae explicatae"*.

Table 1. Continued.

Names as listed in the "*Tabulae explicatae*"	Plate and figure numbers	Names as they appear on the plates	Treatment by Wagner if different from that by Spix, with additional comments in square brackets
Achatina pulchella Spix	Pl. IX, fig. 2	[see *Achatina pavonina*]	Synonym of *Bulimus undatus* Bruguière, 1789. *Buccinum zebra* Müller, 1774, among other names, listed in synonymy, but Bruguière's name retained as valid.
Achatina floccosa Spix	Pl. IX, figs. 3, 4	[see *Achatina pavonina*]	Placed in *Bulimus* as *Bulimus floccosus* "Wagn." [= (Spix)].
Columna maritima Spix	Pl. X, fig. 1	COLUMNA 1. maritima. 2. 8-gyrata. 3. bulimea. 4. sylvatica. 5. LYMNAEUS papyraceus.	Synonym of "*Bulimus calcareus* Bruguière" [= *Helix calcareus* Born, 1778].
Columna 8-*gyrata* Spix	Pl. X, fig. 2	[see *Columna maritima*]	Synonym of "*Bulimus calcareus* Bruguière" [= *Helix calcareus* Born, 1778].
Columna bulimea Spix	Pl. X, fig. 3	[see *Columna maritima*]	Replaced by *Bulimus spixii* Wagner.
Bulimus Spixii Wagner	Pl. X, fig. 3	[see *Columna maritima*]	[Unnecessary replacement name for *Columna bulimea* Spix; junior objective synonym of *C. bulimea* Spix.]
Columna sylvatica Spix	Pl. X, fig. 4	[see *Columna maritima*]	Placed in *Bulimus as Bulimus sylvaticus* "Wagner" [= (Spix)].
Lymnaeus papyraceus Spix	Pl. X, fig. 5	[see *Columna maritima*]	Spix's original spelling, "*Lymnaeus papyraceus*" (legend of plate X) changed to "*Limnaeus papyraceus* Spix". [*Limnaeus* Pfeiffer, 1821 (emendation of *Limneus* Draparnaud, 1801, *Limnus* Montfort, 1810, and *Lymnaeus* Brand, 1810) is a junior synonym of *Lymnaea* Lamarck, 1799.]
Strophocheilus Haemastromus Spix	Pl. XI, fig. 1	STROPHOCHEILUS 1. Haemastomus. 2. 3. Almeida.	Synonym of "*Bulimus ovatus* Bruguière" [= *Helix ovata* Müller, 1774].
Strophocheilus Almeida Spix	Pl. XI, figs. 2, 3	[see *Srophocheilus Haemastomus*]	Synonym of "*Bulimus virgineus* Bruguière, 1789" [= *Helix pudica* Müller, 1774].
Auris melastoma Spix	Pl. XII, figs. 1, 2	AURIS 1. 2. Melastoma. 3. signata. 4. vittata.	Not a new name but a reference to *Bulimus melastomus* Swainson, 1820; emended to "*Bulimus melanostomus* Swainson", citing the original name together with the emended name, the latter used as valid. [Wagner's emendation was unjustified, so *Bulimus mealnostomus* Wagner is an available, junior objective synonym of *Bulimus melastomus* Swainson, 1820 (*Code*, Article 33.2.3).]
Auris signata Spix	Pl. XII, fig. 3	[see *Auris melastoma*]	Placed in *Auricula* as *Auricula signata* "Wagner" [= (Spix)]; compared with *Auricula sileni* Férussac, 1807.
Auris vittata Spix	Pl. XII, fig. 4	[see *Auris melastoma*]	Faded specimen of *Auricula signata* Spix.
Stenostoma auritum Spix	Pl. XIII, figs. 1, 2	STENOSTOMA 1. 2. auritum. 3. Purú. 4. Capueira.	Synonym of *Auricula leporis* "Lamarck" [= "Bruguière", in Férussac, 1807].
Stenostoma Puru Spix	Pl. XIII, fig. 3	[see *Stenostoma auritum*]	Replaced by *Bulimus angulatus* Wagner. The name Purú was printed with a written accent in the plate legend but without an accent in the *Tabulae explicatae* (Puru).
Bulimus angulatus Wagner	Pl. XIII, fig. 3	[see *Stenostoma auritum*]	[Unnecessary replacement name for *Stenostoma puru* Spix; junior objective synonym of *Stenostoma puru* Spix. Spix's name is the name of the Purú River, in apposition; perhaps Wagner considered such a name unacceptable, since he replaced both such names of Spix (see *B. angiostomus*, below).]
Stenostoma Capueira Spix	Pl. XIII, fig. 4	[see *Stenostoma auritum*]	Replaced by *Bulimus angiostomus* Wagner.
Bulimus angiostomus Wagner	Pl. XIII, fig. 4	[see *Stenostoma auritum*]	[Unnecessary replacement name for *Stenostoma capueira* Spix; junior objective synonym of *Stenostoma capueira* Spix. Spix's name is the name of the Capueira River, in apposition. See *B. angulatus*, above.]

Table 1. Continued.

Names as listed in the *"Tabulae explicatae"*	Plate and figure numbers	Names as they appear on the plates	Treatment by Wagner if different from that by Spix, with additional comments in square brackets
Clausilia exesa Spix	Pl. XIV, fig. 1	CLAUSILIA 1. exesa. 2. striata. 3. 6-dentata. 4. pupoides.	Placed in *Pupa* as *Pupa exesa* "Wagner" [= (Spix)].
Clausilia striata Spix	Pl. XIV, fig. 2	[see *Clausilia exesa*]	Placed in *Pupa* as *Pupa striata* "Wagner" [= (Spix)].
Clausilia 6-dentata Spix	Pl. XIV, fig. 3	[see *Clausilia exesa*]	Placed in *Pupa* as *Pupa sexdentata* "Wagner" [= (Spix)].
Clausilia pupoides Spix	Pl. XIV, fig. 4	[see *Clausilia exesa*]	Replaced by *Pupa inflata* Wagner.
Pupa inflata Wagner	Pl. XIV, fig. 4	[see *Clausilia exesa*]	Compared to *Clausilia sexdentata* Spix. [Unnecessary replacement name for *Clausilia pupoides* Spix; junior objective synonym of *Clausilia pupoides* Spix.]
Pupa elatior Spix	Pl. XV, fig. 1	1. PUPA elatior. 2. 3. NAVICULA fasciata. 4. 5. TOMIGERUS clausus.	
Navicula fasciata Spix	Pl. XV, figs. 2, 3	[see *Pupa elatior*]	Replaced by *Helix navicula* Wagner. [The genus-group name *Navicula* Spix is a junior primary homonym of *Navicula* Blainville, 1825.]
Helix Navicula Wagner	Pl. XV, figs. 2, 3	[see *Pupa elatior*]	[Unnecessary replacement name for *Navicula fasciata* Spix; junior objective synonym of *Navicula fasciata* Spix.]
Tomigerus clausus Spix	Pl. XV, figs. 4, 5	[see *Pupa elatior*]	Placed in *Helix* as *Helix clausa* "Wagner" [= (Spix)].
Helicina Pyramidella Spix	Pl. XVI, figs. 1, 2	HELICINA 1. 2. Pyramidella. 3. 4. fasciata. 5. flava.	Placed in *Helix* as *Helix Pyramidella* "Wagner" [= (Spix)].
Helicina fasciata Spix	Pl. XVI, figs. 3, 4	[see *Helicina Pyramidella*]	Junior primary homonym of *Helicina fasciata* Lamarck, 1822; replaced by *Helicina variabilis* Wagner.
Helicina variabilis Wagner	Pl. XVI, figs. 3, 4	[see *Helicina Pyramidella*]	New replacement name for *Helicina fasciata* Spix.
Helicina flava Spix	Pl. XVI, fig. 5	[see *Helicina Pyramidella*]	Variety of *Helicina variabilis* Wagner.
Solarium Serpens Spix	Pl. XVII, figs. 1, 2	SOLARIUM 1. 2. Serpens. 3. 4. candidum. 5. vitreum. 6. imperforatum. 7. pygmaeum.	Spix's apical (pl. XVII, fig. 1) and basal (pl. XVII, fig. 2) views of this species identified as two distinct but very similar species (see below, and see the discussion of this species in the text).
Helix Pellis serpentis Chemnitz	Pl. XVII, fig. 1	[see *Solarium Serpens*]	The apical view (pl. XVII, fig. 1) of *Solarium serpens* Spix identified by Wagner as *Helix pellisserpentis* "Chemnitz" [= Gmelin, 1794, since Chemnitz is unavailable].
Helix punctata Wagner	Pl. XVII, fig. 2	[see *Solarium Serpens*]	New name for *Solarium serpens* Spix of pl. XVII, fig. 2 (non Spix of pl. XVII, fig. 1). [Junior primary homonym of *Helix punctata* Müller, 1774.]
Solarium candidum Spix	Pl. XVII, figs. 3, 4	[see *Solarium Serpens*]	[see *Helix perspectiva*, below]
Solarium vitreum Spix	Pl. XVII, fig. 5	[see *Solarium Serpens*]	[see *Helix perspectiva*, below]
Helix perspectiva Wagner	Pl. XVII, figs. 3–5	[see *Solarium Serpens*]	*Solarium candidum* Spix and *S. vitreum* Spix listed as adult (*"testa completa adulta"*) and younger (*"testa junior"*) specimens, respectively of *Helix perspectiva* Wagner. [Junior primary homonym of *Helix perspectiva* Megerle, 1816, and *Helix perspectiva* Say, 1817. As first revisers, we treat *Helix perspectiva* Wagner as an unnecessary new name for *Solarium candidum* Spix, not for *S. vitreum* Spix. *Helix perspectiva* Wagner is therefore a junior objective synonym of *S. candidum* Spix, and *Solarium vitreum* Spix is a junior subjective synonym of *S. candidum* Spix, according to Wagner's opinion.]
Solarium imperforatum Spix	Pl. XVII, fig. 6	[see *Solarium Serpens*]	Replaced by *Helix vitrina* Wagner.

Table 1. Continued.

Names as listed in the *"Tabulae explicatae"*	Plate and figure numbers	Names as they appear on the plates	Treatment by Wagner if different from that by Spix, with additional comments in square brackets
Helix vitrina Wagner	Pl. XVII, fig. 6	[see *Solarium Serpens*]	[Unnecessary replacement name for *Solarium imperforatum* Spix; junior objective synonym of *Solarium imperforatum* Spix.]
Solarium pygmaeum Spix	Pl. XVII, fig. 7	[see *Solarium Serpens*]	Replaced by *Helix nana* Wagner.
Helix nana Wagner	Pl. XVII, fig. 7	[see *Solarium Serpens*]	[Junior primary homonym of *Helix nana* Martens, 1824, and *Helix nana* Megerle, 1824. Unnecessary replacement name for *Solarium pygmaeum* Spix; junior objective synonym of *Solarium pygmaeum* Spix.]
Planorbis ferrugineus Spix	Pl. XVIII, fig. 1	PLANORBIS 1. ferrugineus. 2. olivaceus. 3. 4. nigricans. 5. albescens. 6. viridis.	Synonym of *Planorbis olivaceus* Spix.
Planorbis olivaceus Wagner and Spix	Pl. XVIII, fig. 2	[see *Planorbis ferrugineus*]	Compared to *"Planorbis corneus"* [= *Helix cornea* Linnaeus, 1758]. [The only claim of joint authorship is in the *"Tabulae explicatae"*. However, no author is mentioned for this species in the text (p. 26); if there was a reason for this departure, it is not evident from the work itself, and species authorship is therefore assignable to Spix alone.]
Planorbis nigricans Spix	Pl. XVIII, figs. 3, 4	[see *Planorbis ferrugineus*]	[see *Planorbis lugubris*, below]
Planorbis albescens Spix	Pl. XVIII, fig. 5	[see *Planorbis ferrugineus*]	[see *Planorbis lugubris*, below]
Planorbis viridis Spix	Pl. XVIII, fig. 6	[see *Planorbis ferrugineus*]	[see *Planorbis lugubris*, below]
Planorbis lugubris Wagner	Pl. XVIII, figs. 3–6	[see *Planorbis ferrugineus*]	*Planorbis nigricans* Spix, *P. albescens* Spix, and *P. viridis* Spix considered as juvenile specimens of *P. lugubris* Wagner. Compared to *"Planorbis corneus"* [= *Helix cornea* Linnaeus, 1758]. [Unnecessary replacement name. *Planorbis nigricans* Spix is the first of the three names listed as *Planorbis lugubris* Wagner in the *"Tabulae explicatae"*. We, as first revisers, take *P. lugubris* Wagner to be the replacement name for *P. nigricans*; the former is thus a junior objective synonym of the latter. *Planorbis albescens* Spix and *P. viridis* Spix are then subjective synonyms according to Wagner's opinion.]
BIVALVIA (see footnote)			
Anodon giganteus Spix	Pl. XIX, figs. 1, 2	ANODON giganteum. 1. juv. 2. adult.	*Anodon crassus* Swainson, 1823, considered a variety of this species, even though Swainson's name has priority.
Anodon trapezeus Spix	Pl. XX, fig. 1	ANODON 1. trapezeum. 2. 4. rotundum.	
Anodon rotundus Spix	Pl. XX, figs. 2–4	[see *Anodon trapezeus*]	*Anodon membranaceus* [= *Mytilus memranaceus* Maton, 1811] given as a synonym, but Spix's name retained as valid. Compared to *Anodon trapezeus* Spix.
Anodon anserinus Spix	Pl. XXI, figs. 1, 2	ANODON anserinum.	Compard to *Anodon giganteus* Spix. [Though the figures have numbers 1 (outer view) and 2 (inner view of both valves), the legend does not mention any numbers].
Anodon longinus Spix	Pl. XXII, fig. 1	ANODON 1. longinum. 2. trigonum. 3. obtusum. 4. lituratum.	
Anodon trigonus Spix	Pl. XXII, fig. 2.	[see *Anodon longinus*]	Compared to *"Anodon sulcatus* Lamarck" [= *Anodonta sulcatus* Lamarck, 1819].
Anodon obtusus Spix	Pl. XXII, fig. 3	[see *Anodon longinus*]	
Anodon lituratus Spix	Pl. XXII, fig. 4	[see *Anodon longinus*]	Synonym (young specimen) of *Anodon obtusus* Spix.

Table 1. Continued.

Names as listed in the *"Tabulae explicatae"*	Plate and figure numbers	Names as they appear on the plates	Treatment by Wagner if different from that by Spix, with additional comments in square brackets
Anodon radiatus Spix	Pl. XXIII, fig. 1	ANODON 1. radiatum. 2. siliquosum. 3. 4. pygmaeum.	Compared to *"Anodon glaucus* Humboldt" [= *Anodonta glaucus* Valenciennes, 1827].
Anodon siliquosus Spix	Pl. XXIII, fig. 2	[see *Anodon radiatus*]	Compared to *Anodon longinus* Spix.
Anodon pygmaeus Spix	Pl. XXIII, figs. 3, 4	[see *Anodon radiatus*]	Synonym (young specimen) of *Anodon siliquosus* Spix.
Anodon ensiformis Spix	Pl. XXIV, figs. 1, 2	ANODON ensiforme.	[Though the figures have numbers 1 (outer view) and 2 (inner view of both valves), the legend does not mention any numbers].
Aplodon inermis Spix	Pl. XXV, figs. 1, 2	1. 2. APLODON inerme. 3. 4. TETRAPLODON pectinatum. 5. 6. CYCLAS bahiensis.	Possible synonym of *Anodon rotundus* Spix.
Tetraplodon pectinatus Spix	Pl. XXV, figs. 3, 4	[see *Anodon inermis*]	Placed in *Unio* as *Unio pectinatus* "Wagner" [= (Spix)]. *Castalia ambigua* Lamarck, 1819, given as a synonym, but Spix's name retained as valid.
Cyclas bahiensis Wagner	Pl. XXV, figs. 5, 6	[see *Anodon inermis*]	Compared to *Cyclas fontinalis* Draparnaud, 1801. [Authorship should be Spix not Wagner; probably a *lapsus calami*, because the legend on plate XXV reads *"Cyclas bahiensis"* (Spix's original spelling) and the text subtitle on p. 32 reads *"Cyclas bahiensis* Spix".]
Diplodon ellipticus Spix	Pl. XXVI, figs. 1, 2	DIPLODON 1. 2. ellipticum. 3. 4. rotundum.	Placed in *Unio* as *Unio ellipticus* "Wagner" [= (Spix)]. Compared to *Unio pictorum* (Linnaeus, 1758).
Diplodon rotundus Spix	Pl. XXVI, figs. 3, 4	[see *Diplodon ellipticus*]	Placed in *Unio* as *Unio rotundus* "Wagner" [= (Spix)]. *Mya variabilis* Maton, 1811, given as a synonym but Spix's name retained as valid.
Diplodon furcatus Spix	Pl. XXVII, figs. 1, 2	DIPLODON furcatum.	Replaced by *Unio caudatus* Wagner. [No numbers printed either with the figures (outer view and inner view of both valves) or in the legend].
Unio caudatus Wagner	Pl. XXVII, figs. 1, 2	[see *Diplodon furcatus*]	*Hyria avicularis* Lamarck, 1819, given as a synonym but Spix's name retained as valid. [Unnecessary replacement name for *Diplodon furcatus* Spix; junior objective synonym of *Diplodon furcatus* Spix.]
Diplodon rhombeus Spix	Pl. XXVIII, figs. 1, 2	DIPLODON rhombeum.	Placed in *Unio* as *Unio rhombeus* "Wagner" [= (Spix)]. Compared to *Unio peruvianus* Lamarck, 1819. [Though the figures have numbers 1 (outer view) and 2 (inner view of both valves), the legend does not mention any numbers].
Triplodon rugosus Spix	Pl. XXIX, figs. 1, 2	TRIPLODON rugosum.	Placed in *Unio* as *Unio rugosus* "Wagner" [= (Spix)]. Compared to *Hyria corrugata* Lamarck, 1819. [Though the figures have numbers 1 (outer view) and 2 (inner view of both valves), the legend does not mention any numbers].

Note—Most Greek nouns ending in *-on* are neuter. However, the word *-odon* (= tooth) and its derived genera ending in *-odon* are masculine. Spix apparently did not realize the difference and gave neuter endings (*-um* or *-e*) to all species in *Anodon*, *Diplodon*, *Triplodon*, and *Tetraplodon*. All these names are, therefore, incorrect original spellings that were rightly corrected by Wagner in the *"Tabulae explicatae"* and in the text (*Code*, Aritcles 31.2, 32.5, 34.2).

Spix), he provided Spix's species name after the short diagnosis, before describing the species in the longer description. When he combined two of Spix's species as varieties under a single Wagner species (e.g., *Helix lineata* Spix and *Ampullaria figulina* Spix under *Ampullaria lineata* Wagner), or synonymized two of Spix's species (*Ampullaria zonata* Spix and *A. archimedes* Spix under *A. zonata* Wagner), he provided another, still shorter diagnosis on the same line as each of Spix's species names, following the two-line diagnosis, before describing the species in the longer description. We suggest that this reflects the likelihood that Spix left not only the

4. AMPULLARIA PAPYRACEA SPIX. Tab. IV. Fig. 1. 2.

A. testa ovato-globosa, tenuissima, longitudinaliter subtilissime striata, nigro-fusca: umbilico angusto; apertura nigra.

Testa oblongo-ovata, globosa, tenuissima, fragilis; striis longitudinalibus crebris, tenuibus, strias transversas, remotas, obsoletas decussantibus. Anfractus quinque aut sex convexi, ultimus maximus. Spira brevis, striis longitudinalibus profundioribus. Apertura ovato-oblonga; labrum acutum, tenue, margine sinistro subreflexo. Umbilicus angustus, longitudinalis. Color testae nigro — fuscus; ultimus anfractus interdum fascia olivaceo brunnea cinctus. Spirafusco-rubra; apertura nigra.

Longitudo 2 poll. 2 lin; lat. 1 poll. 9 lin.

Habitat in fluviis et stagnis Provinciarum Bahiensis, Pernambucanae et Piauhiensis.

5. AMPULLARIA ROSEA SPIX. Tab. IV. Fig. 3.

A. testa ovata, ventricosa, tenui, pellucida, longitudinaliter striata, perforata, albido-rubella; apertura oblongo-ovata, inferne ampla.

Testa oblongo-ovata, ventricosa, tenuis, pellucida, longitudinaliter striata. Anfractus quinque convexi; ultimus maximus, usque ad medium striis longitudinalibus eleganter ornatus, infra medium laevis. Spira exsertiuscula, obtusa; striis longitudinalibus crebris. Apertura oblongo-ovata, superne anfractu penultimo valde angustata, inferne ampla. Labrum acutum, tenue, margine sinistro subreflexum. Umbilicus angustissimus. Color testae rubello-albidus, margo aperturae sinister roseus.

Longitudo 9 ½ lin.; lat. 7 ½ lin.

Habitat in aquis Brasiliae australioris.

Observatio. Haec species, mihi tantum ex unico specimine cognita, dubie Ampullariis adscribenda est, forsan in Bulimi genus amandanda.

6. AMPULLARIA LINEATA WAGN. Tab. V. Fig. 2 et Tab. IV. Fig. 4.

A. testa ovato-globosa, olivaceo-virente aut lutescente, fasciis obscure purpureis ornata; spira elevata; umbilico mediocri; apertura alba, transversim fasciata.

a) VAR. testa majore, adulta, olivaceo-virente, fasciis purpurascentibus cincta: *Helix lineata Spix, Tab. V. Fig. 2.*

Swainson, Zoological Illustrations. No. 21. Tab. 103.: Ampullaria fasciata.

b) VAR. testa minore lutescente, fasciis fuscis cincta: *Ampullaria figulina, Spix Tab. IV. Fig. 4.*

Figure 4. An example of species descriptions, from p. 3 of the Munich edition of the "*Testacea fluviatilia . . .*".

plates but also the two to three line diagnoses. This concurs with Fechter (1983b) who concluded that Spix produced the lithographs with hand coloration, named the species, and attributed a brief, two-line diagnosis to them, and that Wagner elaborated and completed the descriptions. We are not aware of the particular evidence Fechter based these statements on. However, this same conclusion is elaborated on in a paper by Ihering (1890) on Spix's unionoid type material (see below).

We also consider that Spix provided the legends to the plates, thereby permitting his illustrations to be identified. Comparing the Munich issue (publisher ["Typis"] C. Wolf) and the Leipzig issue (publisher T. O. Weigel) is instructive. The title page of the Leipzig issue has the same wording but slightly different type settings compared to the Munich issue, but it does not have a publication date. Nevertheless, we consider it logical to deduce that the Munich issue was published first, with no changes to Spix's legends, and that Wagner made changes subsequently for the Leipzig issue. Our reasoning is as follows.

The Munich issue has the species names with no attributions of authorship, but the Leipzig issue has attributions included in the legends, but only if Wagner had changed the concept of Spix's species. It also lacks the plate numbers. For instance, in the Munich issue, the legend of plate I reads "AMPULLARIA Gigas" [on line 1] and "Tab. I." [line 2]; and, because Wagner made no change to this species, the legend in the Leipzig issue simply reads "AMPULLARIA Gigas", in the same type, but lacks "Tab. I.". In contrast, the Munich issue legend of plate 2 reads "AMPULLARIA 1. zonata. 2. Archimedes" [line 1] and "Tab. II." [line 2], but because Wagner synonymized two of Spix's species, the Leipzig issue legend reads "AMPULLARIA zonata. Wgr. [= Wagner]" on line 1 and "A. 1. zonata. 2. Archimedes. Sp. [= Spix]" on line 2, with the plate number lacking. Similar alterations can be seen on other plates.

Additional instances also suggest that the Munich issue retained Spix's original legends. For example, in the Munich issue, the legend on plate XIX reads "*Anodon giganteum*", but "*Anodon giganteus* Spix" in the "*Tabulae explicatae*" and on text page 27, the latter name with the masculine ending being correct (see footnote to Table 1). When Wagner referred to one of Spix's plates, he gave the incorrect original name, although he used the correct masculine names in the subtitle for each species. For instance, on page 30, Wagner treated *Anodon obtusus* and *Anodon siliquosus*, but he mentioned as varieties or forms the names *Anodon obtusum* Spix, *Anodon lituratum* Spix, *Anodon siliquosum* Spix, and *Anodon pygmaeum* Spix. This indicates that Spix engraved the (incorrect) names on the original plates. Wagner's action in correcting the species endings was mandatory, and does not affect Spix's authorship (*Code*, Article 34.2).

Although Spix's name does not appear on the plates, all these examples strongly suggest that Spix provided both the original plates and legends. For the Munich issue, Wagner, for whatever reason, did not change the legends to reflect his text, whereas, apparently later, for the Leipzig issue, he changed the legends so that they did now reflect his text.

Did Wagner work entirely from Spix's lithographs, with no reference to the shells, or did he see at least some of the shells? Ihering (1890) has argued that Wagner only had access to the lithographs and did not work with the material. He based this deduction on a comparison of the original type material in ZSM in 1888–1889 (i.e., before the partial destruction of Spix's type material during World War II) with Wagner's descriptions in the 1827 volume. Ihering noted not only that measurements were sometimes inaccurate but also that Wagner had made what appeared to Ihering (1890: 119) to be an unbelievable error in terms of the orientation of the bivalve shells. In fact some of the printed lithographs are reversed (e.g., *Aplodon inerme* Spix on pl. XXV figs. 1–2, *Anodon trigonus* Spix on pl. XXII fig. 2, and *Diplodon ellipticus* Spix on pl. XXVI figs. 1–2, as discussed by Ihering 1890: 126–127, 162, and 163–165, respectively). Lithographs are mirror images of the actual plates, and perhaps the engraver assumed that the bivalve halves were alike and engraved some of the figures without taking the trouble to reverse them (the gastropods are illustrated correctly). Wagner, apparently not realizing this, erroneously gave left for right and vice versa, and, accordingly, anterior/posterior and the wrong dentition on the valves of the bivalve shells. Furthermore, Ihering noted that a comparison of Spix's Latin diagnoses (based on the actual type material) with Wagner's more elaborate descriptions shows that the latter made mistakes that were derived from errors introduced in the illustrations, that is, features in the illustrations that are not actually seen on the shells. Ihering therefore concluded that Wagner had not seen the shells.

At the time, Wagner was working in Erlangen and there is no definitive evidence that he actually worked in the Munich collection of Spix until 1832 (see above). However, Wagner's comments on some species strongly suggest that he had access to the shells. For example, Wagner occasionally mentioned that he knew a species of Spix only from Spix's figure (e.g., *Ampullaria archimedes*). On p. 19, Wagner stated that "*Ceterum Pupam exesam, cum in Museo Monacensi specimen nullum adsit, accuratis describere non possum*" (Because there is no specimen in the Munich Museum, I cannot accurately describe *Pupa exesa*). The description of *Bulimus gallinasultana* (p. 9) ends with a reference to Lamarck, which is justified by Wagner, who says: "*Speciminibus, nescio quo casu, in Museo Monacensi omnino deficientibus, hunc Bulimum rarissimum, pretiotissimum non describere possum*" (Because all specimens in the Munich Museum—I do not know why—are totally defective, I cannot describe this very rare and most beautiful *Bulimus*). This means that, when the Munich Museum did not have adequate material, Wagner was not able to elaborate a description, and so he included only the two-line diagnosis, probably provided by Spix (*Pupa exesa*), or copied Lamarck's description (*Bulimus gallinasul-*

tana). Thus, for those species for which Wagner gave his own full description, or for which he did not explicitly state that he had not seen specimens, he had arguably seen the actual material.

Regarding *Bulimus floccosus* [= *Achatina floccosa* Spix], Wagner stated that "*Museum Monacense possidet specimen unicum, cujus apex abruptus est; itaque numerum anfractorum et longitudinem totius testae non indicare possum*" (The Munich Museum has only one specimen, the apex of which is broken; so I cannot indicate either the number of whorls or the total length of the shell). However, Spix's figures 3 and 4 on plate IX do not show a broken apex; perhaps the shell was damaged during its shipping or handling, before Wagner had the opportunity of measuring it. This also implies that shell measurements given by Wagner were probably not taken from the lithographs but from the actual shells.

In some instances Wagner made unambiguous statements that could probably not have been made had he not studied the collection. For example, on p. 31, he said that "*Anodon siliquosum et pygmaeum cl. Spixii aetate sola inter se diversa esse plurimus speciminibus intermediis, quae in Museo Monachensi asservatur, facile probatur*" (*Anodon siliquosum* and *pygmaeum* of the eminent Spix only differ from each other by their age, as can be easily demonstrated by the many intermediate specimens conserved in the Munich Museum). On the same page, Wagner made the following comment on *Anodon radiatus* Spix: "*Museum Monachense permulta specimina hujus speciei asservat, quae omnia ab Anodonte glauco cl. Humboldtii diversa sunt*" (The Munich Museum conserves a lot of specimens of this species, all of which differ from *Anodon glaucus* of the eminent Humboldt).

The instance of *Solarium serpens* Spix is also intriguing. Wagner divided the genus *Helix* into three sections: a) *dentatae, non carinatae* (with apertural teeth, not carinated); b) *carinatae*, and c) *planorbes, neque carinatae, neque dentatae* (planorbid, neither carinated, nor toothed). He placed *Helix punctata* Wagner [= *Solarium serpens* Spix of pl. XVII fig. 2] in section b (*carinatae*), while *Helix pellisserpentis* "Chemnitz" [= *Solarium serpens* Spix of pl. XVII fig. 1] was placed in section c. However, Spix's illustrations are of apical (Spix's fig. 1) and basal (Spix's fig. 2) views, from which it is not possible to determine whether the shell was carinate or not, suggesting that if he was not simply guessing Wagner saw the shell(s).

So, Wagner introduced some severe errors in the description of the bivalves, which induced Ihering (1890) to conclude that he had not seen the specimens. However, the above discussion leads us to conclude that he did indeed work with at least the greater part of Spix's type material, though perhaps not all it.

TYPES

The natural history material collected by Spix and Martius in Brazil formed a major part of what was intended as the "Museum Brasiliense" (Fittkau, 1983). The zoological material and the types were later integrated into the collection of the Zoologische Staatssammlung in Munich, where most of it is still held. Fechter (1983a, b) surveyed the molluscan types of Spix, listing 64 gastropod species and 19 species of Unionoidea, collected, illustrated and named by Spix, as evidenced by the labels and the 1827 publication. However, some of the type material is now missing, as a result of damage the museum suffered during World War II. Also, Spix's original labels are not all extant, and according to Fechter (1983a) it was only possible in four cases, by comparing the labels to letters written by Wagner, to attribute some of the existing older labels to Wagner, apparently stemming from his working in the collection years after Spix's death (see above).

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The genus *Olivancillaria* (Gastropoda: Olividae) in the Miocene of Chile: rediscovery of a senior synonym and description of a new species

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ABSTRACT

Revision of historical collections from the Tertiary of Chile housed in Paris and in new collections in Santiago de Chile revealed the presence of an undescribed species of the olivid genus *Olivancillaria* d'Orbigny, 1840. Also, the used name of a common Miocene species, *O. tumorifera* (Hupé, 1854), is preceded by an almost completely ignored senior synonym. The older and therefore valid name for the known species is reintroduced as *O. claneophila* (Duclos, 1835), status and repository of type material is given, types are redescribed and figured and the new species *O. matanzana* is described. *Olivancillaria matanzana* differs from *O. claneophila* in having a higher spire, a less thick callus, and by lacking a node on the callus.

INTRODUCTION

Only one species of the genus *Olivancillaria* d'Orbigny, 1840, has been described from the Chilean Miocene; that species is generally known as *Oliva tumorifera* Hupé, 1854. It is a common species of moderate local biostratigraphic potential because it occurs in almost all Miocene localities of Chile and is easily recognized. Thus it might help field geologists to date sediments on a provisional basis. Subsequent workers (e.g. Philippi, 1887; Möricke, 1896) used the name *O. tumorifera*, and only later Klappenbach (1966) realized that an earlier name existed for the species. This, however, remained unnoticed by subsequent workers (Fleming in Watters and Fleming, 1972; Tavera, 1979). Discovery of a new species of *Olivancillaria* in the Matanzas collection of V. Covacevich and D. Frassinetti in the Museo Nacional de Historia Natural, Santiago de Chile, initiated a deeper interest in this genus and lead to the rediscovery of the older name for the known species: *Oliva claneophila* Duclos, 1835.

The genus *Olivancillaria* d'Orbigny is usually referred either to the year 1839 (e.g. Rios, 1994; Pastorino, 1995) or 1841 (e.g. Kantor, 1991). However, Burch and Burch (1964) showed the correct date to be 1840. Species of *Olivancillaria* today live predominantly along the Atlantic coast of South America but one species occurs also in India. Fleming (1972) discussed *Olivancillaria* as an Atlantic element in the Miocene fauna of Chile, but a wide distribution in the Pacific during the Miocene is indicated by the presence of *O. altenai* Beets, 1986 in the late Miocene of East Borneo (Beets, 1986). This formerly wide distribution explains the disjunctive Recent distribution in South America and India. *Olivancillaria* must have migrated from Chile across or around South America during the Miocene, but it is unknown where it survived during the Pliocene because there is no record of post-Miocene species from Chile and, on the other hand, there is no Neogene fossil record in Argentina. The genus is also absent in the Caribbean faunas from Neogene to Recent.

Olivancillaria claneophila has been found at almost all Miocene localities from the Navidad Region (Duclos in Chenu, 1846; Philippi, 1887; my own data) to Chiloé Island (Fleming, 1972; my own data). The new species has been found at a locality described by Frassinetti and Covacevich (1993) who, in an earlier paper (Covacevich and Frassinetti, 1980), also provided a preliminary list of the mollusk species encountered there. The fossiliferous level is situated on the tidal platform about one kilometer north of Matanzas (33°57′27″ S, W 71°52′15″ W) and is normally covered by beach-sand. The sediments range from mudstone to sandstone and yield a fauna somewhat unusual for the region, since a number of taxa are only known from this locality. The reason for this, however, is still unresolved. Macrofauna and sediments seem to indicate deposition in a near-coast environment, while benthic foraminifera and ostracods show that displacement into great depths (>1500 m) occurred (Finger et al., 2003).

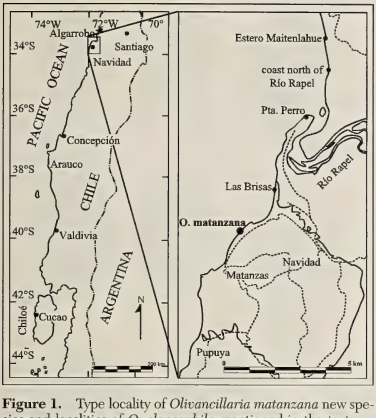

Figure 1. Type locality of *Olivancillaria matanzana* new species and localities of *O. claneophila* mentioned in the text.

The age of the Navidad Formation is still in debate. While some authors suggested a lower Miocene (Dremel in Herm, 1969; Tavera, 1979; Frassinetti and Covacevich, 1993) others gave an upper Miocene age (Tsuchi et al., 1990; Ibaraki, 1992) for the same locality. Both estimates where made with Foraminifera, the former also on the basis of mollusks. Dating of own foraminifer material (Finger et al., 2003) indicates a Late Miocene age for the localities containing *O. claneophila.*

MATERIALS AND METHODS

Specimens described or mentioned in this study are deposited in the collections of the following institutions: Museo Nacional de Historia Natural, Departamento de Paleontología de Invertebrados, Santiago de Chile (SGO.PI); Muséum national d'Histoire naturelle, Laboratoire de Biologie des Invertébrés marins et Malacologie (MNHN-BIMM); Laboratoire de Géologie (MNHN-LG), Paris, France and Senckenberg Museum Frankfurt am Main (SMF), Germany.

SYSTEMATICS

Family Olividae Latreille, 1825
Genus *Olivancillaria* d'Orbigny, 1840

Type Species: *Oliva brasiliensis* Chemnitz, 1788 (= *Porphyria urceus* Röding, 1798); Recent, Brazil to Argentina.

Olivancillaria claneophila (Duclos, 1835)
(Figures 2–7, 14–18)

Oliva claneophila Duclos, 1835: pl. 29, figs. 8, 9; Duclos in Chenu, 1846: 31, pl. 31, figs. 8, 9.
Oliva tumorifera Hupé, 1854: 217–218, Conch. pl. 3, fig. 8; Philippi, 1887: 72, pl. 8, fig. 9.
Oliva pyriformis Philippi, 1887: 73, pl. 8, fig. 11.
Oliva lebuensis Philippi, 1887: 73, pl. 8, fig. 13.
Oliva otaeguii Philippi, 1887: 74, pl. 8, fig. 21.
Ancillaria tumorifera (Hupé, 1854) Möricke, 1896: 572.
Olivancillaria tumorifera (Philippi, 1887) Ihering, 1907: 514; Tavera, 1979: 90, pl. 16, fig. 43.
Olivancillaria claneophila (Duclos, 1835) Klappenbach, 1966: 77.
Olivancillaria (Lintricula) tumorifera (Hupé, 1854) Fleming, 1972: 398, figs. 6t, 6w.

Diagnosis: Shell elongate-oval with convex to angulated sides, solid; spire low, covered by thick callus. Columella with two prominent folds, upper fold splitting into four finer folds in juveniles. Heavy parietal callus with low, well-defined node. Suture channeled apparently only on three quarters of last whorl. Aperture subrectangular.

Description: The solid, elongate-oval shell has convex to angulated sides and is characterized by its low spire with very heavily developed callus. The callus covers the spire whorls completely and about one whorl of callus is visible. The columella is covered by callus, the lower part bearing two moderately prominent folds, of which the upper feathers into four finer ones in juveniles. The parietal-field produced by callus, bears a low, well-defined node. The suture is channeled but due to the heavy callus only visible on the last three quarters of the body whorl. The aperture is sub-rectangular.

Type Material: The specimen figured by Duclos is deposited in MNHN-BIMM (Figure 5, unnumbered, Navidad, height 35.4 mm). The specimen it is here regarded as holotype because there is no indication that he had seen other material. Holotype of *O. tumorifera* MNHN-LG Gg2002/75 (Figures 2–4, Topocalma, height 31.4 mm). Holotype of *O. otaegui* SGO.PI.541 (Figures 14–15, Curauma, height 21 mm). Holotype of *O. lebuensis* SGO.PI.528 (Figure 16, Lebu, height 25 mm). Holotype of *O. pyriformis* SGO.PI.532 (Figures 17–18, locality unknown, height 33 mm).

Other Material Examined: Three specimens from the coast north of Río Rapel, Navidad Formation; 23 specimens from Punta Perro, Navidad Formation; five specimens from Las Brisas, Navidad Formation; four specimens from Matanzas, Navidad Formation; one specimen from southern coast of Peninsula Chocoi near Carelmapu; 29 specimens from Cucao, Chiloé Island (all own collections). SMF 236001 (1 specimen, Punta Perro), SMF 326002 (20 specimens, north of Río Rapel), SGO.PI.5495 (6 specimens, Punta Perro), SGO.PI.5498 (13 specimens, Estero Maitenlahue), SGO.PI.5528 (1 specimen, Rapel Norte), SGO.PI.5533 (2 specimens, Rapel Norte), SGO.PI.5550 (1 specimen, Rapel Norte), SGO.PI.5568 (1 specimen, Rapel Norte), SGO.PI.5577 (7 specimens, Rapel Norte).

Type Locality: The coast near Navidad. "Fossile du

Figures 2–18. Miocene *Olivancillaria* from Chile. **2–7.** *Olivancillaria claneophila*. **2–4.** Holotype of *Oliva tumorifera* Hupé, 1854, MNHN-LG Gg2002/75. **5.** Holotype of *Oliva claneophila* Duclos, 1835, MNHN-BIMM unnumbered. **6–7.** Juvenile specimen from Rapel, SMF 326001. **8–13.** *Olivancillaria matanzana* new species. **8–10.** Holotype, SGO.PI.6008. **11.** Paratype 1, SGO.PI.6009. **12–13.** Paratype 2, SGO.PI.6009. **14–18.** *Olivancillaria claneophila*. **14–15.** Holotype of *Oliva otaegui* Philippi, 1887, SGO.PI.541. **16.** Holotype of *Oliva lebuensis* Philippi, 1887, SGO.PI.528. **17–18.** Holotype of *Oliva pyriformis* Philippi, 1887, SGO.PI.532. Note that specimen in Figure 5 is uncoated while all others are coated with magnesium oxide.

Chili (. . .) il appartient au terrain tertiaire recouvrant le granit de la Trinidad, canton de la Navidad, et ne se rencontre que sur les escarpements des bords de la mer" (Duclos in Chenu, 1846, p. 31).

Occurrence: Southern Peru (DeVries and Frassinetti, 2003) to Chiloé, southern Chile (Fleming, 1972; own data); lowermost to upper Miocene.

Discussion: Of the South American species, *Olivancillaria claneophila* most resembles *O. deshayesiana* (Ducros de Saint Germain, 1857) in having convex whorls and a low spire. It differs from that species through the presence of a callus node on the parietal area. *Olivancillaria claneophila* also resembles *O. carcellesi* Klappenbach, 1965, as figured by Pastorino (1995). From this it differs in its broader, heavier shell, a concave columella and a well-defined node on the parietal callus. *Olivancillaria vesica* (Gmelin, 1791) differs from *O. claneophila* in having more convex whorls, especially in adult specimens. It also has a node on the parietal callus, but a bigger and less defined one. *Olivancillaria vesica* has a narrower spire, an upward-projecting inner-lip callus and the columella is angulated at about half height, all these features cannot be observed in *O. claneophila*. *Olivancillaria urceus*, type species of the genus, has a conical shell with an almost flat spire and slightly convex sides, while *O. claneophila* has a more angulated shell with a low, heavily calloused spire.

The type specimens of *O. lebuensis* and *O. pyriformis* are not well preserved but comparison with the available material, containing specimens of a wide range of preservation quality, confirms the synonymy. The prominent groove on both specimens resembles a pseudolivid groove (see Vermeij, 1998; Nielsen and Frassinetti, 2003); that groove, however, seems to represent a preservation artifact.

Olivancillaria matanzana new species
(Figures 8–13)

Diagnosis: Shell elliptic with convex to angulated sides; spire moderately high, covered by callus. Columella with prominent fold, above it a second one, splitting into four finer folds in juveniles. Strong parietal cal-

lus. Suture about three quarters of the last whorl channeled.

Description: The elliptic shell has convex sides and is characterized by its moderately high spire with well-developed callus covering the spire whorls. The columella is covered by callus, the lower part bears two moderately prominent folds, of which the upper splits into four finer ones in juveniles. The suture is channeled but due to the heavy callus only visible on the last three quarters of the body whorl.

Type Material: Holotype SGO.PI.6008 (Figures 8–10, Matanzas, height 40.9 mm), four paratypes SGO.PI.6009 (Figures 11–13, Matanzas).

Other Material Examined: Further ca. 20 specimens (unnumbered) present in the Matanzas collection of Frassinetti and Covacevich (SGO.PI).

Type Locality: Intertidal platform about 1 km north of Matanzas, Navidad Formation, Central Chile.

Occurrence: Only known from type locality, upper Miocene.

Etymology: After the type locality near the village of Matanzas.

Discussion: *Olivancillaria matanzana* has a higher spire and a thinner callus on it than *O. claneophila*. It also lacks a prominent node on the parietal callus. No intermediate forms have been found. Both species occur together at the Matanzas locality, but *O. matanzana* is known from nowhere else. *Olivancillaria matanzana* resembles *O. carcellesi* even more than *O. claneophila*, but *O. carcellesi* has a high aperture, almost as high as the shell, while *O. claneophila* and *O. matanzana* have lower apertures. *Olivancillaria vesica* has a narrower and lower spire than *O. matanzana*.

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CONTENTS

M. G. Harasewych — New Columbariinae (Gastropoda: Turbinellidae) from the Indian Ocean 93

M. González-Wangüemert
A. Pérez-Ruzafa
M. J. Rosique
A. Ortiz — Genetic differentiation in two cryptic species of Ostreidae, *Ostrea edulis* (Linnaeus, 1758) and *Ostreola stentina* (Payraudeau, 1826) in Mar Menor Lagoon, southwestern Mediterranean Sea 103

Diego G. Zelaya — The genus *Margarella* Thiele, 1893 (Gastropoda: Trochidae) in the southwestern Atlantic Ocean 112

Carlos S. Gallardo
Cristian Manque
Marcela Filún — Comparative resistance to starvation among early juveniles of some marine muricoidean snails 121

Elizabeth C. Davis
Kathryn E. Perez
Daniel J. Bennett — *Euglandina rosea* (Férussac, 1821) is found on the ground and in trees in Florida 127

Gonçalo Calado — Rediscovery of the syntypes of *Doriopsilla pelseneeri* D'Oliveira, 1895 129

New Columbariinae (Gastropoda: Turbinellidae) from the Indian Ocean

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ABSTRACT

Four new species of Columbariinae are described from the Indian Ocean, based on museum material. *Coluzea kallistropha* inhabits the lower continental slope off Mozambique and the KwaZulu-Natal coast of South Africa, and may easily be distinguished from its congeners by its lower spire and broad, flange-like peripheral keel. *Coluzea madagascarensis* occurs on the upper continental slope along the southwestern coast of Madagascar. Diagnostic features include long, radial spines along the shell periphery and strong spiral sculpture. *Columbarium quadrativaricosum* is presently known only from the upper continental slope off Transkei, South Africa. Its distinctive, thick, squarish varices serve to distinguish it from closely related species. *Coluzea naxa* is known only from its type locality along the uppermost continental slope off the Northwest Shelf of Western Australia. It is readily discerned from its geographically proximal congeners on the basis of its smaller, thinner, shell, prominent rounded axial sculpture, and posteriorly directed spines.

INTRODUCTION

The subfamily Columbariinae represents an early [Maestrichtian (Darragh, 1969)] and diverse radiation of vermivorous Turbinellidae that has, since the Neogene, been restricted to habitats ranging from outer continental shelf to abyssal depths along continental margins. The subfamily is currently known from 52 Recent species and subspecies, with greatest diversity occurring along the western margins of ocean basins [western Atlantic Ocean = 11 species; western Indian Ocean = 14 species (3 new herein); western Pacific = 17 species and subspecies]. Six species (1 new herein) are presently known from the eastern Indian Ocean, and single species have been described from the eastern Pacific, the Antarctic, and the Bering Sea. The taxa described herein are based on specimens collected by the research vessels Anton Bruun, Mascareignes III, Meiring Naudé, and Lady Basten and housed in the collections of the National Museum of Natural History, Smithsonian Institution (USNM), the Museum national d'Histoire naturelle, Paris (MNHN), the Natal Museum, Pietermaritzburg (NM), and the Western Australian Museum (WAM). While the increased sampling of soft bottom deep-sea habitats is likely to continue to bring additional columbariine taxa to light, the known fauna is beginning to provide insights into patterns of allopatric speciation and bathymetric zonation, as well as to common ecophenotypic adaptations in different oceans.

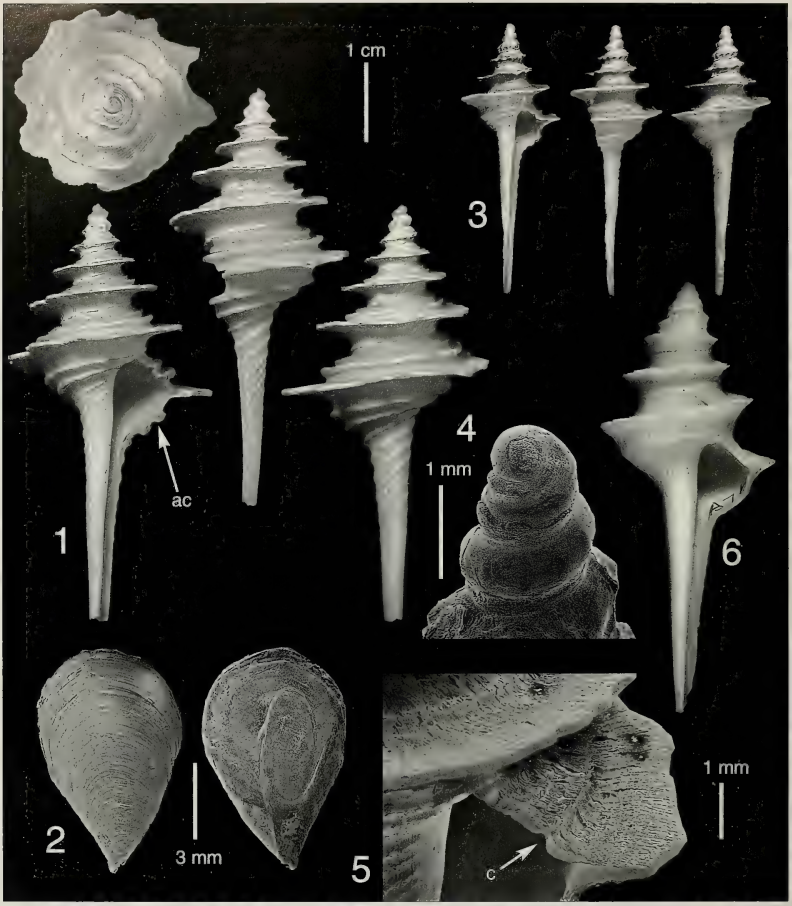
SYSTEMATICS

Family Turbinellidae Swainson, 1840
Subfamily Columbariinae Tomlin, 1928
Genus *Coluzea* Allan, 1926

Coluzea kallistropha new species
(Figures 1–7)

Diagnosis: A moderate sized species with a narrow, fusiform, white shell with a broad, laterally oriented, flange-like keel along the shell periphery with an undulating edge and spiral threads along both surfaces. A weak but distinct anterior carina is present. Shoulder sloping. Spiral sculpture consists of 1–2 strong, rectangular, widely spaced spiral cords between the suture and the periphery, 1–3 cords between periphery and siphonal canal, and 5–8 along the proximal portion of the long, axial siphonal canal. Inner lip formed of a smooth glaze deposited after the outer shell layer of the previous whorl is resorbed.

Description: Shell (Figures 1, 3, 6) of moderate size (to 52 mm), thin to moderately heavy, fusiform; spire angle 35–43°. Protoconch (Figure 4) eroded, estimated to consist of 1½ inflated whorl, first whorl deflected from coiling axis of shell by 75–85°. Transition to teleoconch indistinct, eroded. Teleoconch extrapolated to consist of 8 strongly convex nearly triangular whorls. Suture abutted to previous whorl just anterior to strong cord forming anterior carina (Figure 1, ac). Earliest discernible sculpture consists of strong axial ribs (10 per whorl on



Figures 1–6. *Coluzea kallistropha* new species. **1–2.** Holotype [USNM 718517], 60 mi NE Ponta São Sebastião, Mozambique, 21°18′ S, 36°18′ E, in 1510–1600 m. **1.** Apertural, right lateral, dorsal, and apical views of shell. **2.** Outer and inner surfaces of operculum. **3–5.** Paratype 1 [USNM 717921] 100 mi SE Lourenco Marques, Mozambique, 27°09′ S, 34°09′ E, in 1335 m. **3.** Apertural, right lateral, and dorsal views of shell. **4.** Lateral view of protoconch and early whorls. **5.** Periostracum between suture and shell periphery. **6.** Paratype 2 [NM A76] Durban Bay, from dredgings dumped at head of bay. Scale bar (1 cm) applies to all entire shells. Abbreviations: ac, anterior carina, c, spiral cord.

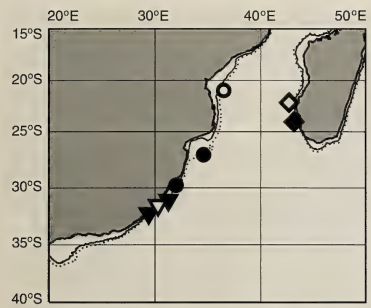


Figure 7. Geographic distributions of new species of *Coluzea* and *Columbarium* from the western Indian Ocean. *Coluzea kallistropha* new species, open circle = type locality, solid circles = additional localities. *Coluzea madagascarensis* new species, open diamond = type locality, solid diamonds = additional localities. *Columbarium quadrativaricosum* new species, open triangle = type locality, solid triangles = additional localities.

second teleoconch whorl) crossed by strong spiral cords (3 above and 3 below periphery). By third teleoconch whorl, short, broad, open, laterally directed spines form along periphery. By fourth teleoconch whorl, axial ribs diminish in prominence; spines fuse to form continuous peripheral keel with 3 weaker spiral cords above, and two below the keel. By fifth teleoconch whorl, axial sculpture becomes indistinct except for fine growth lines, keel increases in size. Spiral sculpture becomes more pronounced, with 1–2 strong hollow cords between suture and periphery, 1–3 between periphery and siphonal canal, 5–8 along proximal portion of siphonal canal, decreasing in prominence distally. Finer spiral threads (1–3) between adjacent cords, 7–12 undulating threads along adapical and abapical surfaces of peripheral keel. Aperture broadly ovate, roughly triangular, sharply tapering anteriorly, deflected from shell axis by 23–26°. Outer lip glazed, furrows beneath spiral cords, deepest beneath peripheral keel. Inner lip smooth, outer shell layer comprising surface sculpture resorbed along parietal region, columella and siphonal canal prior to deposition of thin porcellaneous glaze. Siphonal canal long, axial, stout, straight. Shell color uniformly white. Periostracum (Figure 5) thin, straw-colored, lamellose and finely hirsute, forming low, broad tufts along spiral cords and threads (Figure 5, c). Operculum (Figure 2) thin, claw-shaped, broadly rounded posteriorly, sharply tapering anteriorly, leading to a terminal nucleus. Inner surface with thin glaze covering anterior region and nucleus, defining rounded attachment region. Soft tissues, radula unknown.

Type Locality: 60 mi NE Ponta São Sebastião, Mozambique, 21°18′ S, 36°18′ E, in 1510–1600 m, Gulf of Mexico Shrimp Trawl, Anton Bruun Cruise 8, sta. 399C, 2 October 1964.

Type Material: Holotype, USNM 718517, 51.35 mm, from the type locality; Paratype 1, USNM 717921, 26.60 mm, 100 mi SE Lourenco Marques, Mozambique, 27°09′ S, 34°09′ E, in 1335 m, Anton Bruun Cruise 7, sta. 374C, 23 August 1964; Paratype 2, NM A76, 42.22 mm, Durban Bay, from dredgings dumped at head of bay, 2 December 1972.

Distribution (Figure 7): The presently known range of this species extends from southern Mozambique southward to KwaZulu-Natal, South Africa, at depths of 1335 to 1600 m.

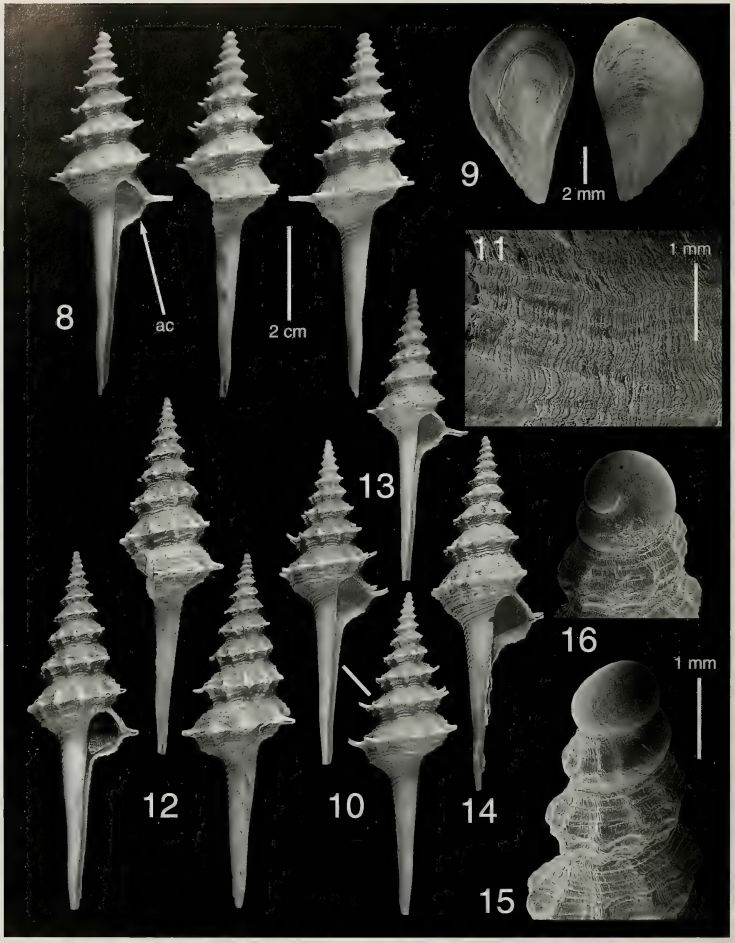
Etymology: *Kallistropha* = *kallimos*—Greek, beautiful + *strophe*—Greek, a turning, twist.

Remarks: *Coluzea kallistropha* is most closely related to *Coluzea eastwoodae* Kilburn, 1971, and *Coluzea juliae* Harasewych, 1989, but may easily be distinguished from both by its broad, flange-like peripheral keel, and by the sculpture between the suture and peripheral keel (smooth in *C. eastwoodae*; 2–3 broad, squarish hollow cords in *C. juliae*; 1–2 strong, narrow cords in *C. kallistropha*). These three species inhabit the same geographic area off the southeastern coast of Africa, but have different bathymetric ranges. *Coluzea eastwoodae,* the most widely sampled species, has been reported from depths ranging from 150 to 740 m, with the deepest live taken specimen presently known being from 570 m. Based on the few specimens of *C. juliae* to be sampled with precise depth data, the confirmed bathymetric range for this species is 600 to 700 m. The two live collected types of *C. kallistropha* were collected along the lower continental slope, at depths of 1335 to 1600 m, among the deepest for any species of Columbariinae. While most living Columbariinae occur on sand and mud bottoms along the outer continental shelf and upper continental slope, two species of *Fulgurofusus, F. benthocallis* (Melvill and Standen, 1907) and *F. aequilonius* Sysoev, 2000, are known to occur on the abyssal plain in polar regions, the former off the South Orkney Islands, the latter in the Bering Sea.

It is interesting to note that a phenotype with a broad, laterally directed, flange-like keel occurs in most regions with a high diversity of columbariines (e.g., *Fulgurofusus brayi* Clench, 1959—western Atlantic; *Coluzea kallistropha*—western Indian Ocean; *Coluzea altocanallis* (Dell, 1956)—New Zealand; *Columbarium pagodoides* (Watson, 1882)—eastern Australia), suggesting that the morphology may be an ecophenotypic response to a particular substrate or habitat.

Coluzea madagascarensis new species
(Figures 7–17)

Diagnosis: A large species, with heavy, narrow, fusiform shell, prominent and persistent strongly shouldered



Figures 8–16. *Coluzea madagascarensis* new species. **8–9.** Holotype [MNHN], off SW Madagascar, 22°18′ S, 43°05′ E, in 450–500 m. **8.** Apertural, right lateral, and dorsal views of shell. **9.** Outer and inner surfaces of operculum. **10–11.** Paratype 1 [USNM 1018395], off SW Madagascar, 22°17′ S, 43°04′ E, in 425–450 m. **10.** Apertural and dorsal views of shell. **11.** Periostracum. **12.** Paratype 2 [MNHN], off SW Madagascar, 22°16′ S, 43°06′ E, in 360–415 m. **13.** Paratype 9. **14.** Paratype 10, both [MNHN], off SW Madagascar, 23°36.4′ S, 43°31.1′ E, in 450–460 m. **15–16.** Views of the protoconch of Paratype 6. [MNHN], off SW Madagascar, 22°14.8′ S, 43°04.7′ E, in 450 m. Scale bar (2 cm) applies to all entire shells.

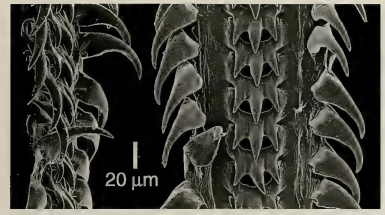


Figure 17. *Coluzea madagascarensis* new species. Left lateral and dorsal views of radular teeth at mid-length of radular ribbon.

axial ribs [9–10 on body whorl], each with a long, axially oriented, open spine along the periphery. Anterior carina weakly developed. Shoulder sloping, with 5–8 distinct cords between suture and periphery, 2–3 between periphery and weak anterior carina, 5–6 between carina and base of siphonal canal, 25–30 along proximal ⅔ of long, axial siphonal canal. Inner lip of smooth glaze deposited after outer shell layer of previous whorl resorbed.

Description: Shell (Figures 8, 10, 12–14) large (to 78 mm), moderately heavy, strongly fusiform; spire angle 28–34°. Protoconch (Figures 15–16) of about 1¼–1½ smooth, glassy, inflated whorls, first whorl smaller than second, deflected from shell axis by about 80°. Transition to teleoconch indistinct, marked by formation of a peripheral keel, followed within ⅛ whorl by axial ribs, then by spiral cords above and below periphery. Teleoconch of up to 10¼ evenly convex whorls with strong peripheral carina bearing tubercles on early whorls that change to long, open, radially oriented spines by sixth postnuclear whorl. Suture abutted to previous whorl just anterior to dominant spiral cord that forms weak anterior carina (Figure 8, ac). Axial sculpture begins within ⅛ whorl of transition to teleoconch, consists of 8–10 strongly shouldered ribs that extend from suture to suture on first teleoconch whorl. Axial ribs overlaid by strong, evenly rounded spiral cords, 3–4 above, 2–3 below periphery. By sixth teleoconch whorl, short, open, spines perpendicular to coiling axis appear along periphery, supporting axial ribs become broader, more prominent near periphery, less so near sutures. As shoulder spines become longer, more pronounced in subsequent whorls [9–10 on body whorl], axial ribs become less discernible. Spiral cords increase in number and prominence with increasing whorl number (body whorl: 5–8 between suture and periphery, 2–3 between periphery and weak anterior carina, 5–6 between carina and base of siphonal canal, 25–30 along proximal ⅔ of siphonal canal, becoming weaker, less distinct distally). Aperture broadly ovate, rounded abaxially, tapering anteriorly, deflected from coiling axis by 26–29°. Outer lip thin. Furrow beneath periphery deepest and widest beneath spines. Second, weaker furrow beneath anterior carina. Inner lip smooth, sculptural elements on outer shell layer resorbed prior to deposition of thin porcellaneous glaze. Siphonal canal long (~0.46 shell length), axial, stout, weakly twisted along distal half. Shell color uniformly white. Periostracum (Figure 11) moderately thick, yellowish brown, of closely spaced lamellae, weakly hirsute along spiral cords (evident in early whorls). Operculum (Figure 9) moderately thin, rounded, tapering to terminal nucleus. Inner surface with rounded glaze along nucleus, surrounding attachment area.

Holotype a mature, poorly preserved, female, with mantle cavity spanning ~¾ whorl, kidney, upper whorls not recovered. Animal light tan colored. Foot, small, rectangular. Retracted tentacles, short, conical; eyes absent. Disposition of mantle cavity and cephalic haemocoel organs similar to *Coluzea aapta* (see Harasewych, 1986:161). Proboscis, long, convoluted within proboscis sheath. Radula (Figure 17) short (3.3 mm), narrow (153 µm), with 116 rows of teeth. Rachidian teeth with 3 short, stout cusps spanning anteriorly indented middle half of basal plate that broadens laterally.

Type Locality: SW Madagascar, 22°18′ S, 43°05′ E, in 450–500 m, Chalutier "Mascareignes III", sta. 33, 20 January 1986.

Type Material: Holotype, MNHN, 77.50 mm, from the type locality; Paratype 1, USNM 1018395, 65.53 mm, SW Madagascar, 22°17′ S, 43°04′ E, in 425–450 m, Chalutier "Mascareignes III", sta. 6, 21 December 1985; Paratype 2, MNHN, 67.50 mm, SW Madagascar, 22°16′ S, 43°06′ E, in 360–415 m, Chalutier "Mascareignes III", sta. 41, 22 January 1986; Paratype 3, MNHN, 78.32 mm, SW Madagascar, 22°14.7′ S, 43°04.5′ E, in 470–475 m, Chalutage 114, 2 December 1973; Paratype 4, MNHN, 72.72 mm, SW Madagascar, 22°18′ S, 43°05′ E, in 425 m, Chalutier "Mascareignes III", sta. 13, 23 December 1985; Paratype 5, MNHN, 54.87 mm, SW Madagascar, 22°21.6′ S, 43°04.3′ E, in 450 m, Chalutage 95, 27 November 1973; Paratype 6, MNHN, 69.62 mm, SW Madagascar, 22°14.8′ S, 43°04.7′ E, in 450 m, Chalutage 115, 2 December 1973; Paratypes 7, 8, MNHN, 58.17 mm, 58.89 mm, SW Madagascar, 22°17.9′ S, 43°04′ E, in 450 m, Chalutage 105, 29 November 1973; Paratypes 9, 10, MNHN, 63.11 mm, 74.05 mm, SW Madagascar, 23°36.4′ S, 43°31.1′ E, in 450–460 m, Chalutage 66, 29 February 1973; Paratype 11, Ritter collection, trawled off Tuléar, Madagascar, in 600–799 m, dead collected, June 2002.

Distribution (Figure 7): *Coluzea madagascarensis* new species occurs off the southwestern coast of Madagascar. The confirmed bathymetric range is 415–470 m, although dead-collected specimens have been taken at depths between 600 and 799 m.

Etymology: *madagascarensis* = Madagascar + *ensis*—Latin, belonging to.

Remarks: *Coluzea madagascarensis* is intermediate in

morphology between *C. eastwoodae* from off southeastern Africa and *C. distephanotis* (Melvill, 1891) from off northwestern Australia, all occurring at comparable depths. It may be distinguished from *C. eastwoodae* by its more elongate, fusiform shell, spiral sculpture that is stronger, more uniform in size and more uniformly distributed (*C. eastwoodae* lacks spiral sculpture between suture and periphery), and by having fewer, longer, axially oriented spines along the periphery. *Coluzea madagascarensis* differs from *C. distephanotis* in having a less tabulate shoulder, stronger spiral sculpture between suture and periphery, and spines that are axially rather than posteriorly directed along the periphery. Both *C. eastwoodae* and *C. distephanotis* have a prominent anterior carina, which is barely distinguishable in *C. madagascarensis*.

Columbarium quadrativaricosum new species
(Figures 7, 18–23)

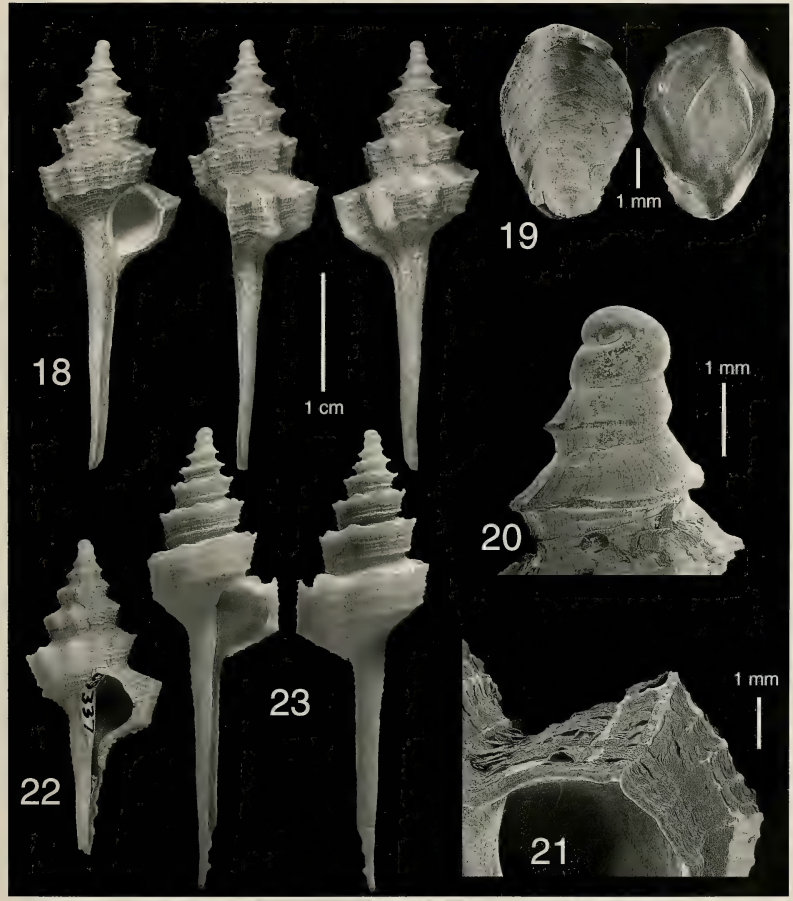
Diagnosis: A small species with a gradate spire, fusiform, white shell, with tabulate, squarish whorls, axial sculpture of thick, rounded varices [8–9 per whorl] and spiral sculpture of distinct cords, square in profile, strongest on periphery and anterior carina. Inner lip formed by a thickly glazed peristomal plate that overlies the columella and proximal siphonal canal.

Description: Shell (Figures 18, 22, 23) small (to 45 mm), thick to moderately thin, fusiform, with squarish varices. Spire angle 46–51°. Protoconch (Figure 20) of about 1½ smooth, glassy whorls. First whorl inflated, deflected from coiling axis by 67–72°. Transition to teleoconch distinguished by onset of peripheral keel, rounded at first, becoming keel-like, with broad, undulating axial nodes within ½ whorl. Teleoconch of up to 7 strongly shouldered, nearly tabulate, squarish whorls. Suture adpressed to previous whorl anterior to anterior carina. Earliest sculpture, apart from very fine growth striae visible on all teleoconch whorls, consists of broad, rounded axial nodes along peripheral keel (8–9 per whorl) that become narrower, more sharply defined, supported by axial ribs of increasing prominence by third teleoconch whorl. By fourth teleoconch whorl, axial ribs form broad, solid varices, thickest between peripheral keel and anterior carina, producing a square whorl profile, with nearly tabulate shoulder. Spiral sculpture first appears on second teleoconch whorl, as single cord below peripheral keel. By third teleoconch whorl, 2–3 weak cords or threads appear above peripheral keel. Body whorl with 4–5 strong, square, equally spaced cords between suture, peripheral keel; 1 strong cord between major cords along peripheral keel, anterior carina; 4–5 cords between anterior carina, siphonal canal; 7–10 cords on proximal ½ of siphonal canal. Finer threads between adjacent cords, suture to keel (0 threads); keel to carina (1–3 threads); carina to siphonal canal (1–2 threads), siphonal canal (0–1 threads). Aperture broadly ovate, nearly rounded, tapering anteriorly, deflected from shell axis by 23–29°. Outer lip thickly glazed, with furrows beneath suture, peripheral keel, anterior carina extending to nearest varix. Inner lip smooth, thickly glazed, peristomal plate overlaying columella, proximal portion of siphonal canal. Siphonal canal long, axial, stout, straight. Shell color uniformly white. Periostracum (Figure 21) thick, amber colored, lamellose. Operculum (Figure 19) thin, ovate, broadly rounded posteriorly, with terminal nucleus. Inner surface with rounded attachment area. Soft tissues, radula, unknown.

Type Locality: Off Mendu Point, Transkei, South Africa, 32°21.8′ S, 29°00.0′ E, in 300 m, on coarse sand, R/V Meiring Naudé, sta. R 10, 12 July 1984.

Type Material: Holotype, NM C 6279, 36.87 mm, from the type locality; Paratype 1, USNM 1018396, 39.79 mm, off Qora River, Transkei Region, Eastern Cape, South Africa, 33°33.6′ S, 28°48.8′ E, in 300 m, coarse sand, some broken shell, R/V Meiring Naudé, sta. U 10, 11 July 1984; Paratype 2, NM C 1802, 28.67 mm, off Bulungula River, Transkei Region, Eastern Cape, South Africa, 32°13.7′ S, 29°08.7′ E, in 250–270 m, muddy sand, old shell debris, R/V Meiring Naudé, sta. 17 July 1982; Paratype 3, NM C 6377, 27.52 mm, off Mendu Point, Transkei Region, Eastern Cape, South Africa, 32°24.0′ S, 28°59.0′ E, in 250 m, coarse sand, rubble, few sponges, R/V Meiring Naudé, sta. R11, 12 July, 1984; Paratypes 4, 5, NM C4911, 44.77 mm, 35.81 mm, off Mendu Point, Transkei Region, Eastern Cape, South Africa, 32°22.6′ S, 29°00.4′ E, in 250–260 m, dredged on coarse sand; R/V Meiring Naudé, sta. R 7, 8 June 1983; Paratype 6, NM C9337, 26.75 mm, off Bulungula River, Transkei Region, Eastern Cape, South Africa, 32°14.0′ S, 9°08.6′ E, in 250–300 m, dredged on coarse sand, R/V Meiring Naudé, sta. O10, 5 June 1985; Paratype 7, NM C6304, 20.02 mm, off Qora River, Transkei Region, Eastern Cape, South Africa, 33°34.2′ S, 28°48.1′ E, in 270 m, dredged on old shell bottom, R/V Meiring Naudé, sta. U 11, 11 July 1984; Paratype 8, NM C6573, 28.40 mm, off Qolora River, Transkei Region, Eastern Cape, South Africa, 32°47.6′ S, 28°36.6′ E, in 510 m, dredged on sandy mud, R/V Meiring Naudé, sta. Y 12, 14 July 1984; Paratype 9, NM C6468, 16.46 mm, off Shixini Point, Transkei Region, Eastern Cape, South Africa, 32°31.4′ S, 28°52.5′ E, in 400–420 m, dredged on coarse sand, fine shell rubble, R/V Meiring Naudé, sta. T 16, 12 July 1984; Paratypes 10, 11, NM C8668, 38.33 mm, 29.35 mm, off Nthlonyane River, Transkei Region, Eastern Cape, South Africa, 32°18.2′ S, 20°06.2′ E, in 550 m, dredged on sand, stones, broken *Dendrophyllia*, R/V Meiring Naudé, sta. P 13, 5 July 1985; Paratype 12, NM C8946, 33.39 mm, off Mgazi River, Transkei Region, Eastern Cape, South Africa, 31°44.3′ S, 29°32.2′ E, in 250 m, dredged on muddy sand, R/V Meiring Naudé, sta. J 11, 4 July 1985.

Distribution (Figure 7): *Columbarium quadrativaricosum* has been collected at multiple stations, all in a narrow range [31°34′–33°34′ S] off the Transkei Region,



Figures 18–23. *Columbarium quadrativaricosum* new species. **18–21.** Holotype [NM C 6279], off Mendu Point, Transkei, South Africa, 32°21.8′ S, 29°00.0′ E, in 300 m. **18.** Apertural, right lateral, and dorsal views of shell. **19.** Outer and inner surfaces of operculum. **20.** Lateral view of the protoconch. **21.** Periostracum. **22.** Paratype 6 [NM C9337], off Bulungula River, Transkei, South Africa, 32°14.0′ S, 9°08.6′ E, in 250–300 m. **23.** Paratype 1 [USNM 1018396], off Qora River, Transkei, South Africa, 33°33.6′ S, 28°48.8′ E, in 300 m. Scale bar (1 cm) applies to all entire shells. Abbreviation: ac, anterior carina.

Eastern Cape, South Africa, at depths ranging from 250 to 550 m. Specimens from depths in excess of 420 m were all dead collected and extremely worn.

Etymology: *quadrativaricosum* = *quadratus*—Latin, squared + *varicosus*—Latin, varicose or ridged.

Remarks: *Columbarium quadrativaricosum* is related to the group of southern African congeners characterized by the presence of thick, rounded varices, including *C. subcontractum* (Sowerby, 1902), *C. formosissimum* Tomlin, 1928, and *C. natalense* Tomlin, 1928. It most closely resembles *C. subcontractum*, which inhabits a similar bathymetric range, but appears to be allopatric, based on limited records that indicate a range to the north of Durban Bay. While these two species reach comparable shell length, *C. quadrativaricosum* has a thinner shell, a proportionally shorter, more gradate spire, a smaller, rounder aperture, a longer, thinner siphonal canal, a tabulate shoulder, and varices that are squarish rather than triangular. It also closely resembles *C. natalense*, which has a comparable geographic range, but inhabits shallower depths [90–160 m]. *Columbarium natalense* can be distinguished from *C. quadrativaricosum* based on its pigmented shell (reddish brown with lighter spiral cords and distal portion of siphonal canal), spiral sculpture of cords that are not continuous, but posteriorly recurved along each varix, the presence of a long, open spine at the shoulder of each varix, and an extremely pronounced cord along the anterior carina. The much larger *C. formosissimum*, which has a more southerly distribution [Cape St. Blaize to Port Alfred] and shallower bathymetric range [121–165 m], may also be distinguished by it heavier proportions more similar to *C. subcontractum*, its reduced or absent spiral sculpture, and its weaker varices that develop at a larger shell size.

Coluzea naxa new species
(Figures 24–30)

Diagnosis: A small species with thin, narrowly fusiform, white shell with gradate spire. Sculpture of strong axial ribs and open, recurved, posteriorly directed spines along shoulder. Spiral sculpture of strong cords that overlay axial ribs, 3 between suture and periphery, 2 between periphery and anterior carina, 4 between anterior carina and siphonal canal, and 12–15 along proximal ⅔ of siphonal canal. Inner lip of thin glaze deposited after columellar surface of previous whorl resorbed.

Description: Shell (Figures 24, 29) small (to 52 mm), thin, narrowly fusiform; spire angle 33–34½°. Protoconch (Figure 26) of about 1½ worn bulbous whorls, first whorl deflected from coiling axis of shell by 80–90°. Transition to teleoconch marked by onset of weak keel along shoulder, forming axial ribs and flanked by spiral cords above and below within first teleoconch whorl. Teleoconch of 9 ⅛ convex, strongly shouldered whorls. Suture abutted to previous whorl just anterior to anterior carina (Figure 24, ac). Axial sculpture initially of 11–13 strong ribs per whorl that originate at the shoulder but do not extend to the anterior carina. Ribs become heavier, increase in number to 18–19 on final whorl, and develop open, curved, posteriorly-directed spines along shoulder by 3rd postnuclear whorl. Spiral sculpture of 3 strong cords between suture and periphery, 2 major cords between periphery and anterior carina, 4 strong cords between anterior carina and siphonal canal, and 12–15 major cords along proximal ⅔ of siphonal canal. One to three weaker cords present between adjacent major cords anterior of shoulder. Aperture broadly ovate, tapering anteriorly, deflected from shell axis by 17°. Outer lip glazed, slightly reflected, forming posteriorly directed, open spine at shoulder. Weak furrows on inner surface of outer lip correspond to shoulder and major spiral cords. Inner lip smooth, surface sculpture resorbed prior to deposition of thin porcellaneous glaze. Siphonal canal long, axial, stout, straight. Shell color uniformly white. Periostracum (Figure 25, per) thin, of overlapping axial lamellae, straw-colored. Operculum (Figure 27) thin, wedge-shaped, broadly rounded posteriorly, sharply tapering anteriorly, slightly concave along right side leading to a terminal nucleus.

Holotype a mature, poorly preserved, desiccated female, with mantle cavity spanning ~¾ whorl, kidney ~½ whorl, upper whorls not recovered. General orientation and morphology of mantle cavity and cephalic hemocoel organs as in *Coluzea aapta* (see Harasewych, 1986:161). Proboscis, long, tightly folded in proboscis sheath, which occupied posterior half of cephalic hemocoel. Radula (Figure 28) short (3.2 mm), narrow (132 μm), with 142 rows of teeth. Lateral teeth monocuspid, recurved, tapering to a point from 20 μm wide attachment area. Rachidian teeth with 3 well-defined, closely spaced, posteriorly-directed cusps emanating from the center of a semicircular basal plate that expands laterally.

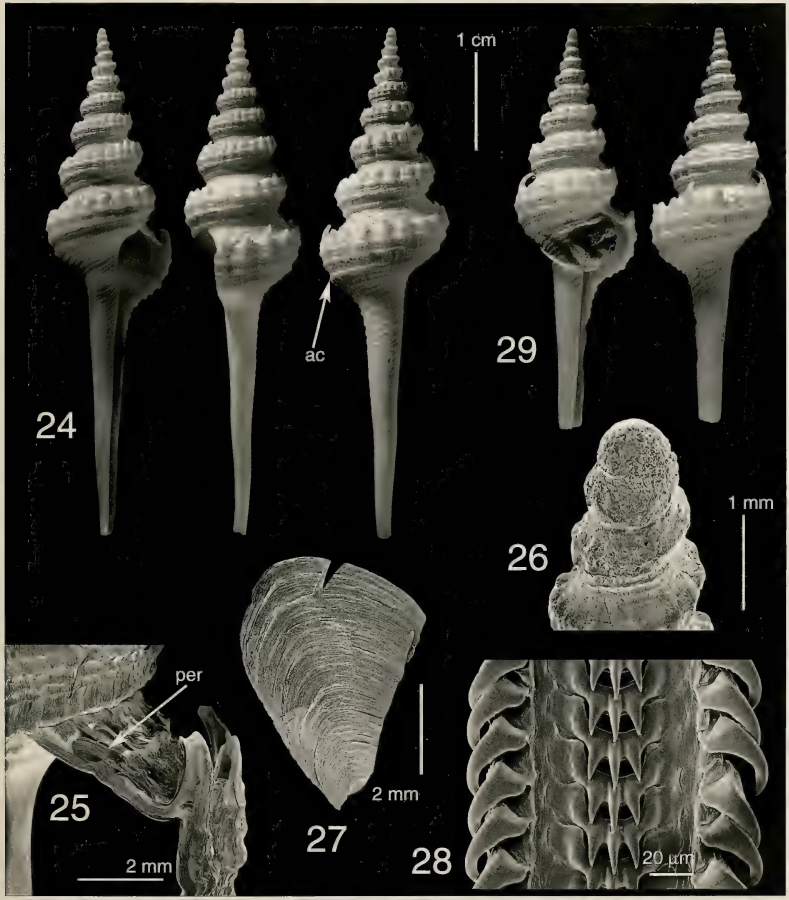
Type Locality (Figure 30): Off Western Australia, North West Shelf, 33 nautical miles S of Bedwell Island, Clerke Reef, 17°46.76′ S, 119°24.6′ W to 17°45.97′ S, 119°25.6′ W, in 250 m, AIMS Survey R/V Lady Basten station LB8, 18 August 1995, Sled dredge, substrate of calcareous mud and worm tubes.

Type Material: Holotype, ♀, WAM S14314, 52.1 mm; Paratype, WAM S14394, 40.1 mm, (with hermit crab), both from the type locality.

Distribution (Figure 30): This species is presently known only from its type locality.

Etymology: *naxa*—Latin, wicker basket with a narrow neck.

Remarks: The narrow, fusiform shell, presence of strong axial ribs that originate at the shoulder but do not extend to the anterior carina, and open, posteriorly reflected spines of *Coluzea naxa* serve to distinguish it from all congeners. *Coluzea naxa* is conchologically most similar to the New Caledonia species, *Coluzea faceta*



Figures 24–29. *Coluzea naxa* new species. Dredged off Western Australia, North West Shelf, 33 nautical miles S of Bedwell Island, Clerke Reef, 17°46.76′ S, 119°24.6′ W to 17°45.97′ S, 119°25.6′ W, in 250 m. **24–28.** Holotype [WAM S14314]. **24.** Apertural, right lateral and dorsal views of shell. **25.** Detail showing periostracum and open spines along shoulder. **26.** Protoconch. **27.** Outer surface of operculum **28.** Dorsal view of mid-section of radular ribbon. **29.** Paratype [WAM S14394]. Scale bar (1 cm) applies to all entire shells. Abbreviations: ac, anterior carina; per, periostracum.

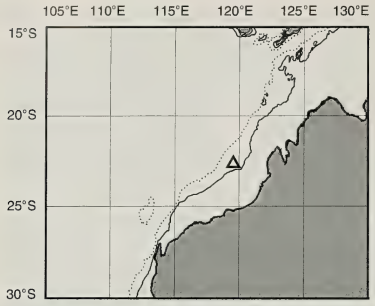


Figure 30. Geographic distribution of *Coluzea naxa* new species, open triangle = type locality.

Harasewych, 1991, which differs in having a larger, heavier shell, with stronger axial ribs that extend beyond the anterior carina, short, laterally directed spines, a broader aperture and narrower shoulder.

Coluzea naxa is easily distinguished from the three geographically more proximal, bathymetrically zoned species *C. distephanotis* (Melvill, 1891), *C. icarus* Harasewych, 1986, and *C. aapta* Harasewych, 1986 [from off Rowley Shoals, Western Australia] by its smaller, thinner, shell, prominent rounded axial sculpture, and posteriorly directed spines. Although *C. distephanotis* was originally described from a depth of 31 m (Melvill, 1891), more recent, better-documented samples indicate that this species inhabits depths in excess of 300 m (Harasewych, 1986), while *C. icarus* and *C. aapta* live at even greater depths along the continental slope. As *Coluzea naxa* is presently known only from a single station at a depth of 250 m, additional sampling will be required to determine the geographic and bathymetric boundaries among these species.

ACKNOWLEDGMENTS

I am grateful to Drs. Dick Kilburn and Dai Herbert (NM), Dr. Philippe Bouchet (MNHN), and Dr. Fred Wells and Correy Whisson (WAM) for making available most of the specimens on which this study was based. Special thanks are due to Dr. Martin Avery Snyder for bringing to my attention the specimens that comprise the type series of *C. naxa*.

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Genetic differentiation in two cryptic species of Ostreidae, *Ostrea edulis* (Linnaeus, 1758) and *Ostreola stentina* (Payraudeau, 1826) in Mar Menor Lagoon, southwestern Mediterranean Sea

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ABSTRACT

Ostrea edulis is a target species for aquaculture but its hatchery has suffered as a result of the lack of morphological differentiation between individuals with a low growth and those that reach commercial size. Two sympatric species of oysters, *Ostrea edulis* and *Ostreola stentina*, have been reported at the Mar Menor Lagoon, Spain. A third nominal species, *Ostreola parenzani*, is now considered a synonym of *O. stentina*. The external morphology of *O. edulis* and *O. stentina* is very similar and this prevents their differentiation at the morphological level, except for maximum size. Oysters were collected from 3 locations along the Mar Menor Lagoon and examined for variation at the *PGI* locus. Principal component analysis of allozyme data revealed the existence of two groups, which confirms the presence of two species: *Ostrea edulis* and *Ostreola stentina*. The genetic variability of the glucose-6-phosphate isomerase (*PGI*) locus was also compared in *Ostrea edulis* and *Ostreola stentina* from the Mar Menor Lagoon. *Ostrea edulis* has high levels of homozygosis and shows an important deviation from the Hardy-Weinberg equilibrium. *Ostreola stentina* shows high heterozygosis and significant differentiation among coastal lagoon samples. The allele frequencies at the *PGI* locus can be used as a diagnostic character at the species level.

INTRODUCTION

Molecular techniques, including cytogenetics (Thiriot-Quiévreux, 1994) and flow cytometry (Partensky et al., 1997), provide a range of methods for quantifying the phylogenetic relationships between species and higher taxa, defining species limits, and identifying and quantifying cryptic species (Féral, 2002).

Biochemical methods helped demonstrate that many abundant and ecologically important "species" are, in fact, groups of species or species complexes (Avise, 1974).

Genetic studies have indicated a remarkably high incidence of cryptic speciation in marine invertebrates (Knowlton, 1993; Thorpe and Solé-Cava, 1994) including marine bivalves (Koehn, 1991; André et al., 1999; Daguin, 2000) and gastropods (Munksgaard, 1990; Palmer et al., 1990; Liu et al., 1991; Corte-Real et al., 1996a; 1996b) and sometimes even in comparatively well studied commercially important species (Yeatman and Benzie, 1994; Chan and Chu, 1996; Thorpe et al., 2000). These genetically differentiated groups often show minor differences in shell morphology that are not always consistent with genetic (allozyme) characters (Sarver et al., 1992). This has important implications for studies on the biology of the involved species. The overlooked presence of cryptic species may produce unexpected variation in physiological or ecological studies.

The demand for high-quality protein, especially from aquatic sources, is rising dramatically. Increased aquaculture production is clearly needed to meet this demand (Dunham et al., 2000). However, aquaculture productivity cannot be optimized if the biological potential of cultured species is not realized. Due to the abovementioned difficulties in differentiating some species on the basis of external morphological characters, the genetic identification and discrimination of aquaculture stocks and species is a fundamental requirement in any culture program (Ferguson, 1994).

Oysters have been exploited since the time of the Roman Empire (Magenis et al., 1983), but harvesting on a large scale began in France around 1850. Spat have been collected from natural beds and cultured with varying success due to epizootic diseases (Jaziri et al., 1987).

In the Mar Menor Lagoon, *Ostrea edulis* have undergone rapid expansion since the early 1980s after the

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artificial enlargement of one of the inlets that connect the lagoon with the Mediterranean. In 1992, 177 million individuals were tallied in a survey with a mean density of 2 oysters/m^2 reaching 22 oysters/m^2 in the most populated areas (Rosique and García-García, 1997). As a result of these high densities, several attempts at hatching were made and the spats of this species have been collected from natural beds and cultured with varying degrees of success due to epizootic diseases and the irregular growth of percentile individuals, which does not allow for profitable exploitation. Blanc et al. (1986) cited a similar finding in Nador Lagoon (Morocco). They studied two populations of oysters that belonged to the same cohort: 49 individuals of a normal growth population and 49 individuals of slow growth. They concluded that the fast-growing sample was *Ostrea edulis.* Of the slow-growing oysters, only 19% were considered to be *Ostrea edulis,* while 81% belonged to another species. Moreover this second species differed from *Ostrea edulis* by three loci and appeared to be a dwarf sibling species of *Ostrea edulis* with similar larvae and spat.

A second species (*Ostreola stentina*) inhabits the Mar Menor Lagoon (Murillo and Talavera, 1983; Olmo and Ros, 1984; Pérez-Ruzafa, 1989) and is undifferentiated from *Ostrea edulis* except for the maximum size reached by each species. A third species, *Ostreola paranzani,* has been reported at the lagoon (Murillo and Talavera, 1983) although it is considered a synonym for *Ostreola stentina* by some authors (Parenzan, 1974).

Ostrea edulis can reach 94 g and 95 mm in weight and size respectively after thirteen months in culture, *Ostreola stentina* does not exceed 20 g in weight and 45 mm in size (Rosique et al., 1995).

Ostrea edulis has a high commercial value and its populations have suffered a strong decline due to overexploitation (Yonge, 1960). It is a hermaphroditic, infralitoral species with a wide geographical distribution along the Atlantic coastline from Norway to Morocco, and all along the Mediterranean as well as the Black Sea (Yonge, 1960; Launey et al., 2002). It has also been introduced into many other parts of the world (e.g., United States, Canada and Japan) due to its aquaculture potential (Korringa, 1976; Launey et al., 2002). Its life history is characterized by fertilisation occurring inside the pallial cavity and the brooding of larvae (Yonge, 1960). As a result of a brooding period of 8 to 10 days, the length of the plankton larval phase is reduced compared to that of other oyster species (Buroker, 1985).

Ostreola stentina is small to medium in size and lives in shallow subtidal waters to a few meters depth, in tropical and temperate seas (Harry, 1985).

The systematic position of Ostreidae has been studied in several works (Pasteur-Humbert, 1962; Harry, 1985; Orton, 1928; Nelson, 1938; Montero, 1971; Stenzel, 1971; Parenzan, 1974) but most of them have not resolved all the taxonomic problems. Harry (1985) presented a good synopsis of the supraspecific classification of living oysters in which he considered not only the structure of the flesh and shells but also the environments, geographic range, and behavior of oysters. The author concluded that the intraspecific variation of oyster shells, which is probably greater than in any other group of living bivalves, precluded the preparation of a simple and satisfactory taxonomic key. The use of molecular genetic techniques in oyster systematics has increased over the past several years, largely due to the increased availability of techniques and increased awareness of the value of genetic data (Littlewood, 1994; Hare and Avise, 1998; Jozefowick and Ó Foighil, 1998; Lee et al., 2000).

Variation in enzyme coding genes has been studied in recent years in several species of marine bivalves, providing differentiation among similar species and information regarding genetic structure in populations of these organisms. Several studies of variations at enzyme loci in *Ostrea edulis* have been made (Wilkins and Mathers, 1973; Buroker, 1982; Maggenis et al., 1983; Johannesson et al., 1989; Le Pennec et al., 1986; Blanc et al., 1986; Saavedra et al., 1987; 1993; 1995; Álvarez et al., 1989). Electrophoretic studies have been mainly restricted to Atlantic populations, which have been very much affected by human harvesting activities (Yonge, 1960; Maggenis, et al., 1983). These studies indicated high genetic uniformity, covering restricted areas of the total range of the species' distribution (Le Pennec et al., 1986; Jaziri et al., 1987; Saavedra et al., 1987). Saavedra et al. (1995) showed that broad macrogeographical clines are a major feature of allozyme interpopulation variability in this species. The origin of these clines probably implied the contact of two Atlantic and Mediterranean oyster stocks that became differentiated in allopatry. Launey et al. (2002) studied the genetic differentiation in *Ostrea edulis* by means of variation at five microsatellite loci. The results showed a mild but significant isolation-by-distance profile, a noticeable between–sample variance in expected heterozygosity, and a tendency for Atlantic populations to be less variable than Mediterranean ones. Comparison with data on allozyme variation in relevant literature confirms this view.

MATERIALS AND METHODS

Study Area

The Mar Menor is a hypersaline coastal lagoon with a surface area of about 135Km^2. It is located in a semi-arid region of the southeast of Spain (37°44′ N, 0°47′ W) on the Mediterranean coast. The mean depth is 3.5 m with a maximum depth of 6 m (Pérez-Ruzafa, 1996). It has five open inlets, which permit the interchange of water with the Mediterranean Sea. In the 1970s, one of these channels (El Estacio) was dredged and widened, inducing important changes in the hydrodynamics and biological communities of the lagoon, including colonization by new species (Pérez-Ruzafa et al., 1987; 1991).

Sampling

In order to analyze the causes of the observed differential growth in oyster populations and to confirm the

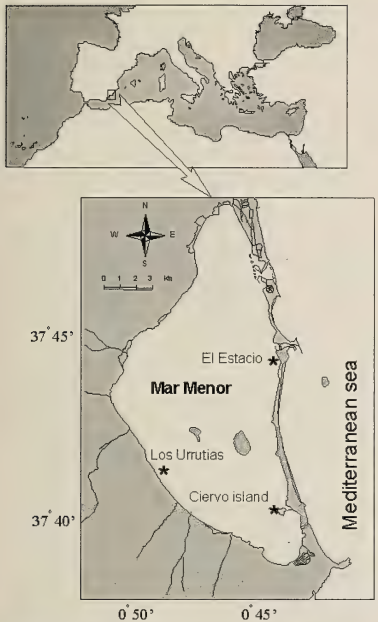

Figure 1. Sampling localities in Mar Menor Lagoon.

existence of the two reported species in the Mar Menor Lagoon, thus determining their importance in oyster hatchery, three localities were sampled at the lagoon in 1996 (Figure 1). Two samples were taken in natural oyster beds at Los Urrutias and Ciervo Island. The third sample was collected as spat at El Estacio in January and moved to aquaculture installations at Marbella (southern Spain) where after 8 months they were collected as adult oysters. This ensures that all individuals belong to the same cohort.

Electrophoresis

All oysters were transported live to the laboratory where they were dissected. Portions of adductor muscle were removed from each individual, homogenized in 1.5M Tris buffer (pH 9), and centrifuged at 4°C and 13500xg. They were stored at −40°C until electrophoresis.

Vertical polyacrylamide gel electrophoresis was carried out at a constant voltage (125 V) for 5 hours at 4°C. Gels were stained for *PGI* activity as described in Harris and Hopkinson (1976) with some modifications in the proportion of reagents (see González-Wangüemert, 1997).

Isozymes were numbered in decreasing order of mobility starting from the most anodal; allozymes were encoded according to the mobility of the most common allele (100).

Population Genetic Analysis: The existence of homogeneous genetic groups was explored performing a Principal Component Analysis (PCA) (ter Braak and Prentice, 1988) on the matrix of genotypes. The results of the ordination analysis are displayed in a biplot, scaling the axes, adjusting genotype scores to genotype variance: the resulting scores are correlations between genotypes and eigenvectors. All these calculations were done using the CANOCO v. 3.15 package (ter Braak, 1990).

The groups identified by the PCA were characterized morphologically comparing the maximum length of the shells (L1) using analyses of variance (ANOVA). According to the results, identified groups were assigned to the species *Ostrea edulis* and *Ostreola stentina*.

The genetic variability of the samples was recorded as expected and observed heterozygosity (H_e and H_o, respectively) and the deviation coefficient were calculated. Differences in gene frequencies among three samples of *Ostreola stentina* were tested using χ^2 test (two degrees of freedom).

To analyze spatial differences in populations, a second PCA analysis was performed on the allelic frequency matrix for the two species and genetic variability descriptors at each locality.

F-statistics following Wright (1951) were calculated to detect non-random mating within populations (F_{IS}) and differentiation between populations (F_{ST}). Both statistics were calculated via the Weir and Cockerham method (1984). Probabilities of random departure from zero for F-values, according to the null hypothesis, were read directly from the distribution of 1000 randomized matrices computed via permutation of individuals among populations. This was performed using the "Genetix" F-testing procedure, thus providing a test of significance.

Genetic distance (Nei's D; Nei, 1978) was computed between pairwise samples. Probabilities of random departure from zero for Nei's D-values, according to the null hypothesis, were read directly from the distribution of 1000 randomized matrices computed by permutation.

Gene flow between samples was estimated as the number of migrants exchanged between populations *per* generation at equilibrium (N_e m). Values for N_e m were derived from one approach with F_{ST} values, following Wright's island model (1951).

The data was analyzed using the Genetix package (Bonhomme et al., 1993) (available at: www.univ-montp2.fr/genome-pop/genetix.htm).

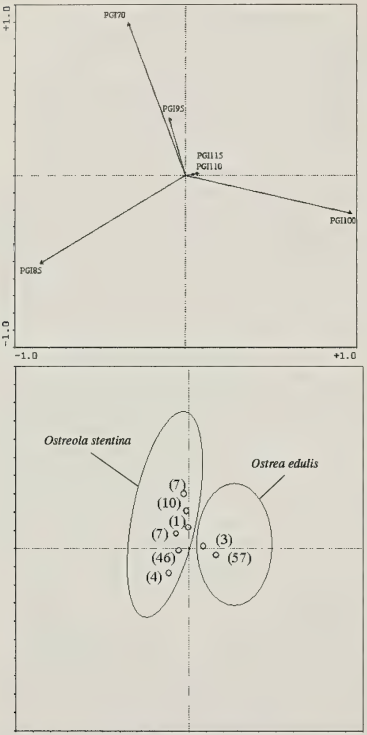

Figure 2. Ordination of first two axes of principal component analysis (PCA) of individual genotypes that jointly explained 91.7% of the variance in the global data set (numbers in brackets correspond to number of individual in that particular point).

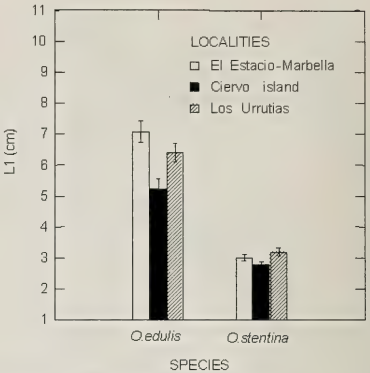

Figure 3. Significant differences in maximum diameter of the shell in the two species of oysters in the three sampling sites in Mar Menor. All individuals grouped as a species in this figure correspond to the individuals of same species in Figure 2 above.

RESULTS

A total of 168 individual oysters have been analyzed for the glucose-6-phosphate isomerase (*PGI*). The electrophoretic survey shows nine different genotypes. The first two axes of the PCA analysis (Figure 2) explain 91% of the total variance in data. The results shows two well-differentiated groups along the first ordination axis, which accounted for most of the variation, explaining 67.2% of the total variance.

The results of the ANOVA performed in order to characterize these groups morphologically show significant differences ($p<0.001$) in maximum size among genetic groups (Figure 3). Group 1 has a mean size of 6.61 cm (± 0.21). Group 2 has a mean size of 3.16 cm (±0.04). The individuals cultivated in Malaga, belonging to the same cohort, show the same significant differences in size which are in line with genetic differentiation. So the two groups, which do not share any alleles, would correspond to the two species reported at the Mar Menor Lagoon, *Ostrea edulis* with only three alleles and three genotypes and *Ostreola stentina* with three alleles and six genotypes, respectively. The relative frequencies of all detected genotypes are shown in Table 1.

PGI was encoded by three alleles in *Ostrea edulis* (Table 2), though only three individuals exhibited the *PGI**115 and one individual showed the allele *PGI**110

Table 1. Relative frequencies of *PGI* genotypes in coastal lagoon oysters.

Genotypes	*Ostrea edulis*	*Ostrea stentina*
N	57	111
°100/100	0.9452	0
°100/115	0.0410	0
°100/110	0.0136	0
°70/70	0	0.0930
°70/85	0	0.3813
°70/95	0	0.1101
°85/85	0	0.3644
°85/95	0	0.0762
°95/95	0	0.0084

Table 2. Allele frequencies at *PGI* locus of *Ostrea edulis* and *Ostreola stentina* (N: number of individuals; EE: El Estacio; IC: Ciervo Island; U: Los Urrutias).

Species	Samples	N	*PGI 70°*	*PGI 85°*	*PGI 95°*	*PGI 100°*	*PGI 110°*	*PGI 115°*
Ostrea edulis	EE	20	0	0	0	0.950	0.025	0.025
	IC	19	0	0	0	1	0	0
	U	18	0	0	0	0.970	0	0.030
	EE	76	0.263	0.645	0.092	0	0	0
	IC	22	0.386	0.568	0.046	0	0	0
Ostreola stentina	U	13	0.385	0.461	0.154	0	0	0

in heterozygous combination (Table 1). The locus can be regarded as essentially monomorphic in this species.

In *Ostreola stentina* three alleles of the phosphoglucose isomerase were expressed with frequencies higher than 0.10, as such the locus can be regarded as polymorphic.

Little difference was detected between the observed and expected heterozygosity. The highest deviation coefficient (D) was 0.0278 for *Ostrea edulis* and 0.111 for *Ostreola stentina* (Table 3). The observed heterozygosity in *Ostrea edulis* showed low values (ranging from 0.00 to 0.0952) due to *PGI*100* being mainly combined as a homozygote and only four individuals being heterozygotes. *Ostreola stentina* has higher observed heterozygosity than *Ostrea edulis*, since 56% of the individuals analyzed were heterozygotes.

Allele frequencies at *PGI* differed significantly among the three sampled populations of *Ostreola stentina* (χ^2=5.99; P=0.035).

The PCA analyses performed on the allelic frequency matrix and genetic variability descriptors at each locality separate both species along the first axis which explains 97.8% of the total variance in data (Figure 4). *Ostrea edulis* samples groups in the positive part of the axis are characterized by a high homozygosity and a low heterozygote deficit. *Ostreola stentina* populations in the negative part are characterized by a higher expected and observed heterozygosity and a high heterozygote deficit. The second axis explains an additional 1.7% of the total variance and discriminates mainly among *Ostreola stentina* populations, with the El Estacio population, closer to the Mediterranean, in the positive part, with a dominance of *PGI* 85° allele, and that of Los Urrutias in the negative part with a dominance of *PGI* 95° allele and a higher heterozygote deficit.

Deviations from Hardy-Weinberg proportions within samples are shown by means of F_{IS} statistic. F_{IS} values indicated a significant heterozygote excess ranging from −0.006 to −0.101 in *Ostreola stentina* (Table 3). *Ostrea edulis* showed a deviation from Hardy-Weinberg expectations within the El Estacio sample, although it was not significant. (Table 3). Nei's genetic distances (Nei, 1978) were estimated using *PGI* locus (Table 4) in *Ostreola stentina*. Values ranged from −0.024 to 0.017. All distances were not significant at the 0.05 level. Estimates of genetic subdivision (F_{ST}) in the three samples are given in Table 4. The minimum positive F_{ST} value derived from allelic variation was found between the El Estacio and Ciervo Island samples (0.008), showing low divergence in gene frequencies between the two populations. In contrast, F_{ST} was considerably higher (0.026) between El Estacio and Los Urrutias samples, suggesting the possible occurrence of restricted gene flow between these populations. F_{ST} values between samples were significant at the 0.05 level.

Assuming equilibrium between genetic drift and migration, we calculated the number of migrants (N_em) *per* generation (Table 5), based on F_{ST} values and according to the island model. Estimates of the number of migrants ranged from 9.16 (El Estacio-Los Urrutias) to infinite (Ciervo Island-Los Urrutias).

DISCUSSION

Allele frequencies at the *PGI* locus, used as a species-diagnosing character, allow the differentiation of the two sympatric oyster species studied. The coexistence of both species could explain the disastrous oyster hatchery attempt in the Mar Menor Lagoon (Rosique et al., 1995).

Table 3. Observed and expected heterozygosities (H_o and H_e), deviation coefficient (D) and F_{IS} (ns: non-significance; *: $p<0.05$; EE: El Estacio; IC: Ciervo Island; U: Los Urrutias).

Species	Samples	H_o	H_e	D	F_{IS}
Ostrea edulis	EE	0.0952	0.0963	−0.0106	0.013 ns
	IC	0	0	0	—
	U	0.0556	0.0540	0.0278	0 ns
	EE	0.5132	0.5066	0.0129	−0.006*
	IC	0.5909	0.5258	0.1101	−0.101*
Ostreola stentina	U	0.6923	0.6154	0.1111	−0.085*

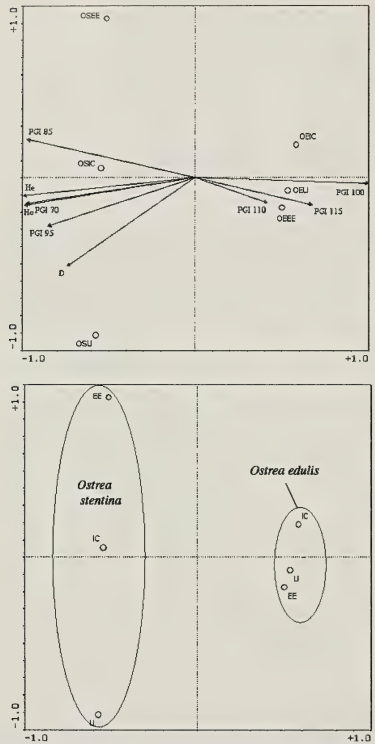

Figure 4. Ordination of first two axes of principal component analysis (PCA) of allele frequencies that jointly explained 99.5% of the variance in the global data set. (EE:, El Estacio; IC: Ciervo Island; U: Los Urrutias).

Genetic variation within and between populations has been demonstrated by the use of electrophoresis. We now have some information regarding the frequencies and distribution of alleles in wild populations of *Ostrea edulis* and *Ostreola stentina* in the Mar Menor Lagoon. Lower levels of genetic variation and heterozygote deficit were detected in the *Ostrea edulis* population.

All the electrophoresis studies on *Ostrea edulis* populations coincide in that this species displays lower levels of allozyme variation than other bivalves (Buroker, 1982; Saavedra et al., 1987) and the overall differentiation among its populations is usually slight (Johannesson et al., 1989). In fact Saavedra et al. (1993) showed, through an UPGMA dendrogram based on Nei's unbiased genetic distances, two main clusters, one formed by the eastern Mediterranean samples and the other by the remaining populations (western Mediterranean and Atlantic samples).

Table 4. Pairwise Nei's genetic distances (below the diagonal) and F_{ST} values (above the diagonal) in *Ostreola stentina*. F_{ST} and Nei's D considered to be significantly different from zero (*) if they fall within the 5% most extreme values in the permutation test. (ns: non-significance; * = $p<0.05$; EE: El Estacio; IC: Cievo Island; U:Los Urrutias).

	EE	IC	U
EE	~	0.082*	0.0266*
IC	0.0080 ns	~	−0.0076*
U	0.017 ns	−0.024 ns	~

Two of the *Ostrea edulis* populations studied (El Estacio and Los Urrutias) have very low observed heterozygosity, though a significant deficit in heterozygotes is not observed. The Ciervo island population has 100% homozygotic individuals, so that this population shows an excessive heterozygote deficit and an important deviation from the Hardy-Weinberg equilibrium.

Some researchers have documented a deficit in heterozygotes for populations of *Ostrea edulis* from Atlantic oyster beds (Buroker, 1982; Maggenis et al., 1983; Johannesson, et al., 1989; Saavedra et al., 1995; Launey et al., 2002). The biological origin of these heterozygote genotype deficiencies may be related to fecundation. This takes place inside the pallial cavity of the female, which favors mating between nearest-neighbors. Also, larvae are brooded for a period of 8 or 10 days before the plankton phase, which limits dispersal. In addition, the extremely low levels of variability detected may to some extent be due to the recent history and exploitation of these populations (Saavedra et al., 1993).

Apart from chance alone, a number of factors may be responsible for causing deficiencies in heterozygotes against the H-W model in allozyme data. These include, null alleles, the Walhund effect, inbreeding and selection against heterozygotes or strong directional selection as a consequence of the geographic isolation of some populations (Zouros and Foltz, 1984; Mamuris et al., 1998; Rossi et al., 1998).

The low levels of observed allozyme variation in the

Table 5. *Ostreola stentina*. Estimates of N_em using F_{ST} values (Wright, 1951) (EE: El Estacio; IC: Ciervo Island; U: Los Urrutias).

	EE	IC	U
EE	~		
IC	30.28	~	
U	9.16		~

Ostrea edulis populations of the Mar Menor Lagoon, may be due to the recent history and exploitation of these populations. The current *Ostrea edulis* oyster bed in the Mar Menor Lagoon could come from oyster beds harvested for commercial purposes in NW Spain (Rosique per. com.). The transplantation of farmed stocks from Atlantic populations to Mediterranean populations has been a common occurrence (Launey et al., 2002). This hypothesis is reinforced due to the fact that the *Ostrea edulis* population from the Mar Menor Lagoon showed a lower heterozygosity than Mediterranean populations, and similar values to Atlantic populations (Arousa and Ares, NW Spain; Saavedra et al., 1993) and those of NW France (Jaziri et al., 1987). Allozyme and microsatellite studies have shown a lower genetic variability in Atlantic populations than in Mediterranean ones. This result could be explained by an overall smaller evolutionary effective size for Atlantic populations compared to Mediterranean populations and two main explanations have been put forward for such a difference: variance in effective sizes and oyster parasites (Launey et al., 2002).

High levels of variation were evident in populations of *Ostreola stentina*. This species shows six different genotypes for phosphoglucose isomerase and a high observed heterozygosity. This high variability could be due to long larval period (Harry, 1985) which could favor the dispersion of the gene pool. Some authors affirm that patterns of variability at the *PGI* locus in bivalves suggest that species inhabiting temporally variable or spatially heterogeneous environments exhibit higher levels of genetic variability than those from less variable or more monotonous environments (Valentine and Ayala, 1978). This agrees with the fact that the Mar Menor Lagoon shows a high degree of isolation with respect to the Mediterranean and highly variable environmental conditions (Pérez-Ruzafa, 1996) explaining the high genetic variability in *Ostreola stentina*.

F_{ST} values among *Ostreola stentina* populations are always lower than 0.1, and although significant, are indicative that there is little divergence among populations (Hartl, 2000). The fact that the Ciervo Island and Los Urrutias localities show infinite rates of interchange of individuals and negative F_{ST} and genetic distance values, suggests that both localities have the same *Ostreola stentina* population. Further genetic studies using several loci are required to confirm this hypothesis.

The results of this study confirm that there are two species (*Ostrea edulis* and *Ostreola stentina*) in the Mar Menor Lagoon stock and the alleles at the *PGI* locus can be used as a species-diagnosing character. As this situation can be a common state in the distribution area of both species, some works related to ecological and physiological adaptations or ecotoxicological responses of any of them should be reviewed. Some marine molluscs regulate their body tissue levels of particular trace metals to constant levels over a wide range of metal levels in their environment (Rainbow et al., 1990). The laboratory experiments have also provided evidence that this regulation is species-specific (Bryan et al., 1985; Rainbow et al., 1990; Dallinger and Rainbow, 1993) so that the existence of two cryptic species could change the conclusions of some toxicological works in *Ostrea edulis* (George et al., 1978; Auffret et al., 2002). Similar considerations could be applied to *Ostrea edulis* physiological studies (Beiras et al., 1995; Labarta et al., 1999; Culloty et al., 2001; Culloty et al., 2002) and works on the resistance of this species to the parasite *Bonamia ostreae* (Elston et al., 1987; Culloty and Mulcahy, 1996; Naciri-Graven et al., 1998; Naciri-Graven et al., 1999).

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The genus *Margarella* Thiele, 1893 (Gastropoda: Trochidae) in the southwestern Atlantic Ocean

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ABSTRACT

The taxonomic status of eight species from the southwestern Atlantic and adjacent sub-Antarctic and Antarctic waters, previously referred to either as *Margarella* or *Margarites* Gray, 1847, is analyzed. The presence of a first marginal tooth of the radula forming a "protolateromarginal" plate, a long afferent membrane in the ctenidium and the presence of antero-lateral expansions on the foot (horn-like projections) clearly indicate that southwestern Atlantic species belong to *Margarella*. On the basis of a morphological analysis of representatives of the genus type species, *Margarella* is redescribed and the genera *Margarites*, *Margarita*, *Margaritella* and *Valvatella* are excluded from the Southwestern Atlantic Ocean list of species. The placement of *Margarella* within the Gibbulini tribe of the subfamily Trochinae is re-affirmed based on anatomical and behavioral observations.

INTRODUCTION

Margarella Thiele, 1893 is a high-latitude, southern hemisphere genus of small size trochoid gastropods living on brown algae or on hard substrata mainly in the intertidal or shallow subtidal. Members of this genus have been formerly described or reported, among others (see below), under the genus *Margarita* Leach, 1819, a synonym of *Margarites* Gray, 1847, a taxon well known as distributed in the northern hemisphere.

A "not rudimentary innermost lateral plate" (i.e. the innermost marginal tooth with a laterally expanded base and a well-developed shaft and cutting edge) was described for *Margarella expansa* (Sowerby, 1838), the type species of the genus. This character was also reported by Dembrosi (1969) as present in *M. violacea* (King and Broderip, 1832), *M. achilles* (Strebel, 1908), *M. tropidophoroides* (Strebel, 1908) and *M. obsoleta* Powell, 1951. Powell (1951) described *Margarella bouvetia* from Bouvet Island, and although he figured the first marginal tooth as a reduced plate (as it is characteristic in the northern hemisphere genus *Margarites*), the species was placed under *Margarella*. Deambrosi (1969) described the first marginal tooth as "rudimentary without cutting edge" in *Margarella antarctica* (Lamy, 1905), *M. bouvetia*, and *M. expansa*, as did Arnaud (1972a) for *Margarella refulgens* (E. A. Smith, 1907) and *Margarella crebrilirulata* (E. A. Smith, 1907). Accordingly, these species were assigned to *Margarites*. From previous literature records both *Margarella* and *Margarites* have been recognized as living in sub-Antarctic and Antarctic waters. In contrast, Hickman and McLean (1990) questioned the presence of *Margarites* in the Southern Hemisphere, and Reid and Osorio (2000), referring to *Margarella sensu lato*, pointed out that "confusion surrounds the specific identification, generic assignment and relationships of Magellanic and Antarctic species".

In the present paper the taxonomic status of species from the southwestern Atlantic and adjacent sub-Antarctic and Antarctic waters, previously referred to *Margarella* and *Margarites*, is analyzed based on the study of the radula, ctenidium, epipodial tentacles, and shell morphology.

MATERIALS AND METHODS

Representatives of eight *Margarella* species from the Magellanic, sub-Antarctic, and Antarctic regions were studied (Table 1). Radulae of adult specimens were dissected, cleaned by rinsing in a sodium hypochlorite solution and appropriately mounted for scanning electron microscopy (SEM). Light microscope radula preparations used by Deambrosi (1969) were re-mounted for analysis under SEM. Radulae from all studied species were figured through SEM and described following Hickman and McLean's (1990) terminology. External anatomy in *Margarella expansa*, *M. violacea*, *M. antarctica*, and *M. steineni* was studied. In addition, live specimens of *Margarella expansa* from Ushuaia, Tierra del Fuego, Argentina, were observed in laboratory conditions.

Voucher specimens are housed at Museo de La Plata (MLP) and Museo Argentino de Ciencias Naturales "Bernandino Rivadavia" (MACN). Photographs of two of the three syntypes of *Margarella violacea* and the ho-

Table 1. Species of *Margarella* examined in this study. (*): only radula preparations made by Deambrosi (1969).

Species	Locality	Repository
Margarella achilles (Strebel, 1908) (*)	?	MLP unnumbered
Margarella antarctica (Lamy, 1905)	Melchior Is., Antarctica	MLP 5623
Margarella bouvetia Powell, 1951 (*)	?	MLP unnumbered
Margarella expansa (Sowerby, 1838) (*)	?	MLP 25241
Margarella expansa (Sowerby, 1838)	Ushuaia, Tierra del Fuego	MLP 7349
Margarella obsoleta Powell, 1951	South Georgia Islands	MACN 13526
Margarella steineni (Strebel, 1905)	South Georgia Islands	MACN 13573
Margarella tropidophoroides Strebel, 1908	South Georgia Islands	MACN 18939
Margarella violacea (King and Broderip, 1832)	Inutil Bay, Magellan Strait	MLP 7350

lotype of *Margarella jason* from the Natural History Museum, London (BMNH) were used for comparative purposes.

SYSTEMATICS

Margarella Thiele, 1893

Margarella Thiele, 1893, p. 406 (replacement name for *Margaritella* Thiele, 1891, p. 259).

Type species by subsequent designation (Thiele, 1924): *Trochus (Photinula) expansus* Sowerby, 1838.

Diagnosis: *Margarella* is characterized by having the first marginal tooth of the radula forming a protolateromarginal plate, dimorphic neck lobes, four pairs of epipodial tentacles emerging from a simple epipodial tissue, and foot expanded in two antero-lateral horn-like projections. The shell is small to medium size, low spired, expanded at the last whorl; the columella is thick, without denticles and interior of shell nacreous.

Morphology and Anatomy of Southwestern Atlantic Species:

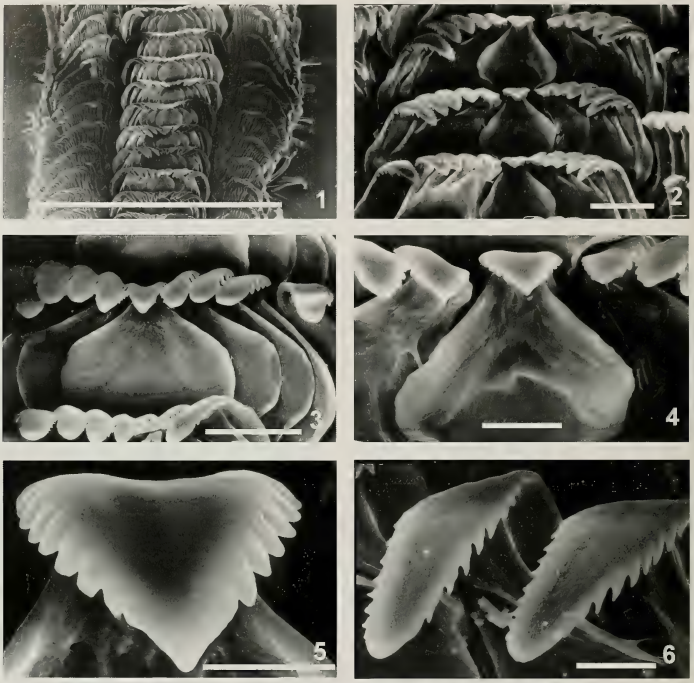
Shell: In the species of *Margarella* examined (Table 1), the shell is small to medium size (up to 22 mm wide), trochoid, usually globose, solid, of up to 4 whorls, with a relatively high whorl increment rate. The protoconch, about 700 μm wide, is smooth, whitish, glossy, with one whorl (Figure 21). The spire is low, with rounded whorls, the last expanded, somewhat globose, sometimes angulate (Figures 23–28). The surface is glossy or dull, smooth or spirally sculptured (Figures 23–28). The aperture is large, rounded, or obliquely ovate. The aperture lip is simple and smooth, and the columella is thick, without denticles. The interior is nacreous. Adult specimens have a wide white columelar callus with a median longitudinal depression. The umbilicus is open in young specimens and may be open or closed in adults (Figures 23–25).

In *M. expansa* the shell is composed of two well-differentiated ultrastructural layers: the outer layer of prismatic crystals, the inner, thicker, with a laminar structure (Figure 22).

All studied species have a circular, multispiral, with a short growing edge, fully corneous, thin and brownish operculum, that can be deeply retracted into the shell.

Radula: All species of *Margarella* examined (Table 1) showed the same general radular morphology: the large, regularly arcuate, bilaterally symmetrical radula is of the rhipidoglossate type; rachidian, lateral, and marginal teeth show characteristically well-developed, overhanging cutting edges (Figure 1). The base of the rachidian tooth has a pyriform outline, sometimes ovate or greatly expanded at the base (Figures 2–4). The M-shaped top of central tooth has a large central cusp, rounded at the tip, and 6–8 narrower and smaller pointed cusps on each side (Figure 5). Each of the five lateral teeth is elongated and of similar shape; their laterally expanded bases overlap; the basal profile is equivalent to the half of that of the central tooth (Figures 2, 3). The tongue-like cutting edge on the lateral tooth is serrated on both sides and slightly asymmetrical, nearly reaching the tip of the cutting edge only on the inner margin (Figure 6). The first marginal tooth has a laterally enlarged base, and a shaft and cutting edge similar to that of the remaining marginal teeth (this tooth element corresponds to the so called protolateromarginal plate) (Figures 7–14). The remaining marginal teeth are numerous (about 40 on each half), long and narrow, with a serrated cusp and a sickle-like-shaped distal end when viewed laterally (Figures 15, 16, 18). Within a row, the marginal teeth are steeply graded in solidness and shape: the innermost are stronger, with well-developed serrated edges and the outermost delicate with more sparsely serrated cutting edges (Figures 15, 16, 18). In posterior view, the bases of the marginal teeth bend in a finely serrated heel; the outer edge of the shaft is serrated, bearing small spines (Figure 17).

Anatomy: Specimens of *Margarella expansa, M. violacea, M. antarctica,* and *M. steineni* were examined. The snout is broad, short, and tubular, with a split ventral lip and the distal end expanded to form an oral disk; the snout projects laterally as two flaps. Small and simple cephalic lappets are present. Long, narrow, and cylindrical cephalic tentacles arise between the base of the cephalic lappets and the stout eyestalks. The right eyestalk bears a long and narrow appendix at its base. The neck lobes are dimorphic: the right one is simple, form-



Figures 1–6. Radula of *Margarella* species. **1.** *M. bouvetia*: general morphology. **2.** *M. expansa*: central and lateral teeth. **3–4.** Details of the central tooth. **3.** *M. steineni*. **4.** *M. expansa*. **5.** *M. violacea*: detail of the cutting edge of central tooth. **6.** *M. steineni*: detail of the cutting edge of a lateral tooth. Scale bars: Figure 1 = 1 mm; Figures 2, 3 = 100 μm; Figures 4, 6 = 20 μm; Figure 5 = 10 μm.

ing the exhalant siphon, the left one bears 1–3 small foliate projections (sometime called "small tentacular filaments"). The epipodium is simple, with four pairs of epipodial tentacles; the tentacles are narrow and long, highly contractile, with a micro-papillated surface; sometimes an additional left unpaired tentacle may be present (Figures 19–20).

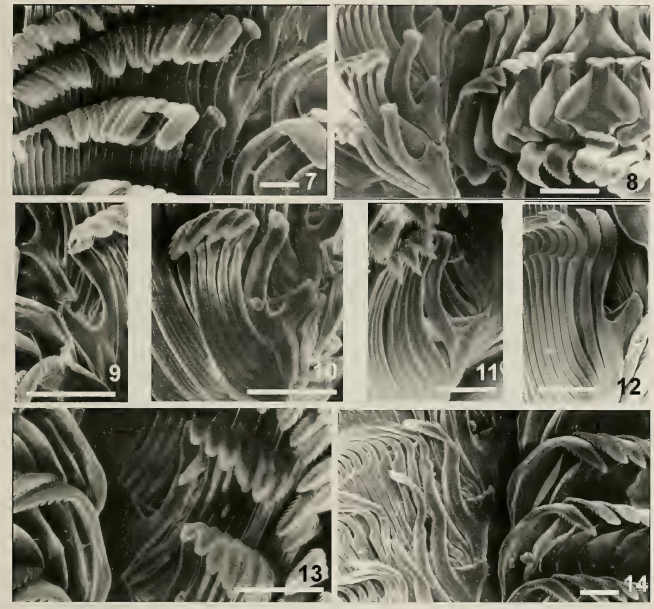
The foot has an anterior truncated end, expanded into two short lateral horn-like projections, which are usually visible also in preserved specimens (Figure 19). In *Margarella expansa* the entire upper surface of the body is pigmented black, while the ventral foot surface is cream.

The bipectinate ctenidium has a relatively long dorsal afferent membrane that surpasses the transverse pallial vein and connects the ctenidial axis to the mantle skirt.

Biological Observations: Specimens of *Margarella expansa* were collected from subtidal to 50 m depth, living mainly on blades and holdfasts of the brown alga *Macrocystis pyrifera*, as well as on rocky or crushed shell substrates.

Laboratory observations revealed that they are able to move floating in upside-down position with the expanded foot gliding onto the inner side of the air-water interface. It was also observed that the foot is able to wrap around algal blades and holdfasts.

Egg masses of *Margarella expansa* were collected from blades of the kelp *Macrocystis pyrifera* in January and November. The largest egg-mass (29 mm in diameter) consisted of a ribbon with about 1600 eggs, measuring 0.51±0.03 mm diameter (n = 33), which adhered

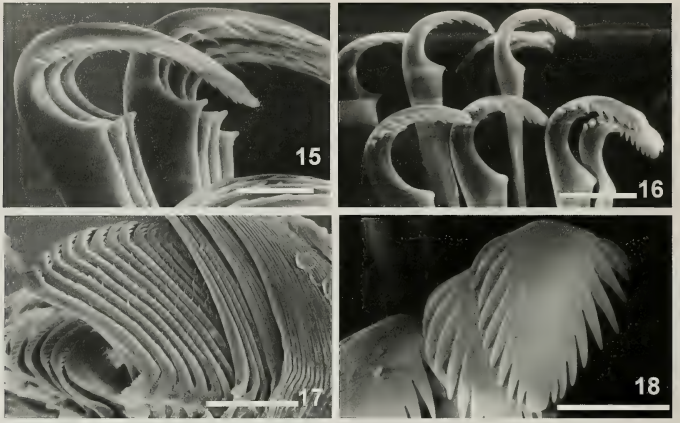


Figures 7–14. Details of first innermost marginal tooth in *Margarella* species. **7.** *M. expansa.* **8.** *M. antarctica.* **9.** *M. tropidophoroides.* **10.** *M. violacea.* **11.** *M. steineni.* **12.** *M. achilles.* **13.** *M. obsoleta.* **14.** *M. bouvetia.* Scale bars: Figures 7–14 = 100 μm.

to the blade surface via a gelatinous matrix, and were arranged in a spiral pattern (Figure 29). Embryos developed within the egg capsule until the stage of crawling juveniles (no free-swimming stage).

Remarks: *Margarella* resembles the genus *Margarites* in shell morphology and in some reproductive features (both spawning benthic egg masses), but in the morphology of the radula and details of external anatomy, both genera clearly differ. The radula of all *Margarella* species studied here consistently differs from that described for *Margarites*, particularly the morphology of the first marginal tooth, variously referred to as a "protolateromarginal plate", "innermost lateral plate" or "lateromarginal plate". Thiele (1929) and Hickman and McLean (1990) recognized the morphology of this tooth as a valuable diagnostic character to separate *Margarites* and *Margarella*. From the present study it is clear that in *Margarella* the innermost marginal tooth undoubtedly corresponds to a protolateromarginal plate as defined by Hickman and McLean (1990) (i.e., a tooth with a base greatly enlarged laterally, but with a well-developed shaft and cutting edge). Conversely, in *Margarites* this tooth (a true lateral plate) is represented by an expanded plate without cutting edge.

The constancy in the number of lateral teeth appears to be an additional character that contributes to the definition of *Margarella*. All *Margarella* species studied here, as well as others for which the radula is known, have five lateral teeth: *Margarella refulgens* (Eales, 1923; Arnaud, 1972a; Numanami, 1996), *Margarella crebrilirulata* (Arnaud, 1972a), *Margarella gunnerusensis* Numanami, 1996 and *Margarella whiteana* Linse, 2002. Conversely, in *Margarites*, the number of lateral teeth varies: four in *Margarites gigantea* (Leche, 1878), five in *Margarites argentata* (Gould, 1841), six in *Margarites helicinus* (Phipps, 1774), *Margarites beringensis* (E. A. Smith, 1899) and *Margarites albolineatus* (E. A. Smith, 1899), and seven in *Margarites hickmanae* McLean, 1984 (McLean, 1984; Hickman and McLean, 1990; Warén, 1990). The lateral teeth in *Margarites* are usually stronger and wider than in *Margarella*.

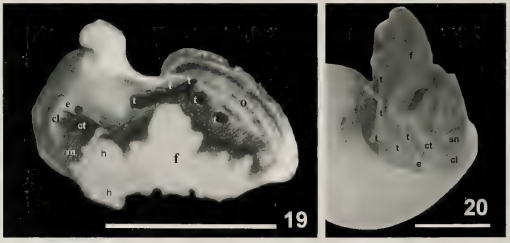


Figures 15–18. Detail of marginal teeth in *Margarella* species. **15–16.** Lateral view of the uppermost part of marginal teeth. **15.** *M.* obsoleta: inner marginals. **16.** *M. expansa*: outer marginals. **17.** *M. expansa*: detail of lateral and basal portion of marginal teeth. **18.** *M. expansa*: detail of the cutting edge. Scale bars: Figures 15, 16 = 20 μm; Figure 17 = 100 μm; Figure 18 = 10 μm.

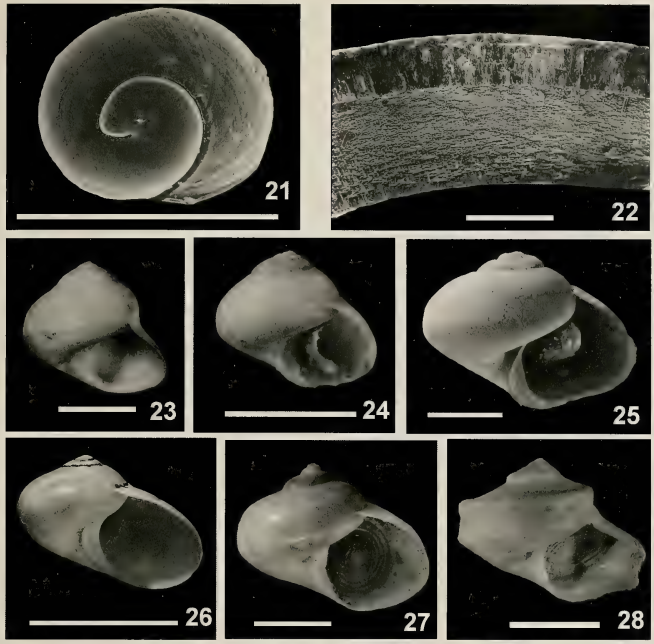
Smith (1879), Pelseneer (1903) and Thiele (1906) considered the asymmetry of the left and right neck lobes as an additional diagnostic character for *Margarella*. All the species studied here showed dimorphic neck lobes.

The ctenidial morphology of southwestern Atlantic species of *Margarella* is studied for the first time. All species examined had a ctenidium with a relatively long afferent membrane, clearly different from that in *Margarites*, in which a short dorsal afferent membrane is restricted to the region posterior to the transverse pallial vein (Hickman and McLean, 1990).

Species of *Margarella* here studied, as well as the Antarctic and sub–Antarctic species *M. crebrilirulata*, *M. expansa*, *M. steineni*, *M. bouvetia*, and *M. achilles* studied by Smith (1879), Powell (1951), Arnaud (1972b) and Numanami (1996), have four pairs of epipodial tentacles, while in *Margarites* the number of epipodial tentacles ranges from five to seven pairs (Kiener, 1880; Hickman and McLean, 1990). However, during the present study specimens of *Margarella expansa* frequently showed an additional left unpaired tentacle, as previously reported by Thiele (1906) for *M. violacea*. Throughout the present study, an additional unpaired



Figures 19–20. External anatomy of *Margarella* species. **19.** *M. violacea*. **20.** *M. steineni*. **cl**: cephalic lappets; **ct**: cephalic tentacles; **e**: eye stalk; **f**: foot; **h**: antero-lateral expansions of the food (horn-like projections); **o**: operculum; **sn**: snout; **t**: epipodial tentacles. Scale bars: Figure 17–18 = 4 mm.



Figures 21–28. Shell morphology of *Margarella* species. **21.** Protoconch of *M. expansa.* **22.** Shell structure of *M. expansa.* **23–24.** Two syntypes of *M. violacea* (BMNH 20020261). **25.** Juvenile specimen of *M. violacea.* **26.** Type specimen of *M. jason* (BMNH 1961348). **27.** *M. obsoleta.* **28.** *M. tropidophoroides.* Scale bars: Figures 21, 25 = 1 mm; Figure 22 = 100 μm; Figures 23, 24, 26 = 5 mm; Figures 27, 28 = 3 mm.

tentacle was also found in *M. steineni* and *M. antarctica.* This observation might explain the discrepancies in the number of epipodial tentacles reported by Powell (1951), Arnaud (1972a), and Numanami (1996) for *Margarella antarctica, M. refulgens,* and *M. gunnerusensis.* Similarly, in *Margarella refulgens,* Arnaud (1972b) reported five and Numanami (1996) four pairs of epipodia. A similar variability in the number of epipodial tentacles is known in the Antarctic trochid *Antimargarita dulcis* as reported by Eales (1923) and *Margarites groenlandica* by Kiener (1880).

Moreover, the foot shape forming lateral horn-like projections during locomotion and the ability to enroll the food around algae in *Margarella* are characters not reported for *Margarites* (Hickman, 1996).

DISCUSSION

Several authors have misinterpreted the morphology of the first marginal tooth in some species from the Southern Ocean (i.e. *Margarella expansa, M. antarctica, M. bouvetia, M. refulgens*), describing it as a lateromarginal plate and, consequently, reporting them under the genus *Margarites.* In the present paper it was possible to restudy and reinterpret from SEM images the morphology of the radula of *Margarella expansa, M. antarctica,* and *M. bouvetia,* which were previously described by Powell (1951), Deambrosi (1969), and Troncoso et al. (2001) from light microscope slide preparations. In all these species, as well as it was observed in this study for *M. achilles, M. obsoleta, M. steineni, M. tropidophoroides,*

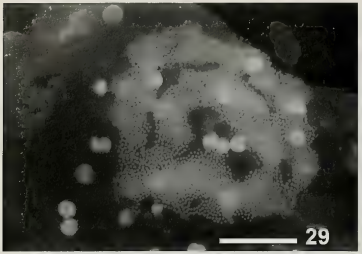


Figure 29. Egg masses of *Margarella violacea.* Scale bar: 10 mm.

and *M. violacea,* the morphology of the first marginal tooth clearly corresponded to that of a protolateromarginal plate. It is evident that discrepancy with previous workers is a consequence of the observational technique used. The *Margarella* radula is very difficult to interpret from light microscope preparations (a technique used mostly in the past) due to the high number of teeth and the high degree of juxtaposition. Numanami (1996) also reported *Margarella refulgens* as *Margarites,* although it is clear that the morphology of the first marginal tooth also corresponds to a protolateromarginal plate (Numanami, 1996, fig. 12F).

The present paper reveals that previous records of the genus *Margarites* (Margaritinae) from the southwestern Atlantic Ocean originated through misinterpretation of the radular characters. The evidence discussed here strongly suggests that the Antarctic species referred to the genus *Margarites* actually belongs to *Margarella.*

Other Genus-level Names Applied to *Margarella*

As it was mentioned above, southwestern Atlantic and Antarctic species of *Margarella* have been frequently reported under *Margarites. Margarita,* a name under which some southern species of *Margarella* were also reported was shown to be a junior synonym of *Margarites* (Keen, 1960; Quinn, 1979); similarly *Valvatella* Gray, 1857, was wrongly used, being presently considered a subgenus of *Margarites* (Hickman and McLean, 1990).

Margaritella, proposed by Thiele (1891) to include *Margarella violacea* and *M. expansa,* is a homonym of *Margaritella* Schmidt, 1880, a genus of hexactinellid sponges. Accordingly, Thiele (1893) proposed *Margarella* as a replacement name.

Trochus (*sensu lato*) Linnaeus, 1758 was frequently and ambiguously used in the old literature to refer to gastropods with trochoid shells and presently included in the families Trochidae and Turbinidae. *Margarella expansa* was described under *Trochus* (*Photinula*), a name subsequently used by Smith (1879) and Watson (1886). *Trochus sensu stricto* is the type genus of the subfamily Trochinae, and is clearly different from *Margarella* (Hickman and McLean, 1990).

Species of *Margarella* have also frequently been referred to *Photinula* H. Adams and A. Adams, 1854 (*nomen novum pro Photina* H. Adams and A. Adams, 1853, non Burmeister, 1838) (Ihering, 1902; Strebel, 1905, 1908). *Photinula sensu stricto,* however, is a member of the Calliostomatinae, clearly differing from *Margarella* in radular morphology, number of epipodial tentacles and honeycomb–like sculpture of protoconch.

Promargarita was proposed by Strebel (1908) as a subgenus of *Photinula* (*s.l.*), but in the same work he considered it as a genus-level name when describing *Promargarita tropidophoroides,* which is actually a species of *Margarella.* Powell (1951) and Keen (1960) considered *Promargarita* as a subgenus of *Margarella* that includes the species from South Georgia Islands with spirally ornamented shells: *M. tropidophoroides, M. achilles,* and *M. obsoleta*; although, this shell character is also present in *Margarella whiteana* from Antarctic Peninsula, Antarctica (Linse, 2002). The validity of *Promargarita* as a subgenus of *Margarella* will be discussed in a future paper, in the context of a systematic revision of the species of the genus.

Lamy (1911) wrongly identified specimens of a true *Margarella* species, probably *M. obsoleta,* from South Georgia Islands as *Photinula* (*Kingotrochus*) *lahillei* var. *carinata.*

Submargarita (type species: *S. impervia*) was described by Strebel (1908), and a number of species were described under *Submargarita*: *S. notalis* (Strebel, 1908), *S. strebeli* Thiele, 1912, *S. similis* Thiele, 1912, *S. mamillata* Thiele, 1912, and *S. unifilosa* Thiele, 1912. Thiele (1929) considered *Submargarita* a subgenus of *Margarella.* Warén (1992) based on radular morphology of *S. notalis* transferred all the above-mentioned Antarctic species (including *S. impervia*) to *Lissotesta* Iredale, 1915, provisionally allocating the genus to the family Skeneideae. Furthermore, a true *Margarella* species, *M. crebrilirulata* from Antarctica, was reported under *Submargarita* by Thiele (1912).

The Suprageneric Placement of *Margarella*

The higher taxonomy of the Trochidae is mainly based on characters of the radula and external anatomy (Hickman and McLean, 1990). Hickman and McLean (1990) proposed three informal clades between the family and subfamily ranks, based on ctenidial morphology, recognizing the radula as diagnostic at subfamily level, and certain characters of the shell and epipodial structures, as diagnostic at the tribe rank. Powell (1951) considered the morphology of the epipodial tentacles as a valuable character in defining genera within the Trochoidea.

The relatively long afferent membrane of the bipectinate ctenidum, the M-shaped top to cusp rachidian tooth and the presence of a protolateromarginal plate, clearly place *Margarella* in the subfamily Trochinae, as

previously suggested by Hickman and McLean (1990), rather than Margaritinae. The ability to wrap the foot around algae is a behavioral character only reported as present in Gibbulini, Trochini, and Cantharidini, but not in other trochid groups, including Margaritini (Hickman, 1996). The relatively low-spire shell, with the aperture lacking columellar denticles, and the presence of epipodial tentacles emerging from simple epipodial tissue, as well as the presence of antero-lateral horn-like projections (according to Hickman (1996) the latter character is only present in the tribe Gibbulini) indicate that *Margarella* belongs to tribe Gibbulini. However, other behavioral character such as the living habit of *Margarella,* commonly reported as living on brown algae, either on blades or associated to their holdfasts (King and Broderip, 1932; Arnaud, 1972b; Ojeda and Santelices, 1984; Castilla, 1985; present study) is not a typical feature among representatives of the Gibbulini (Hickman and Mc Lean, 1990), such mode of life was reported for austral Gibbulini of small size, especially in the genus *Notogibbula* Iredale, 1924 (Hickman and McLean, 1990).

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Comparative resistance to starvation among early juveniles of some marine muricoidean snails

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ABSTRACT

Trophon geversianus is a muricid snail in which juveniles show abundant internal yolk reserves, as well as a 2–3 mm size at hatching which is double that of most of the species within the family. It is thus possible that the resistance of these juveniles to the effects of food deprivation would be significantly greater than that typical of other species in the family. This hypothesis was evaluated experimentally by studying the tolerance of these juveniles to starvation in comparison with juveniles of *Chorus giganteus* and *Acanthina monodon*, which represent the more generalized characteristics found among the muricoideans. Recently hatched snails of the three species were established in aquaria with flow-through seawater and no food sources. Three replicate systems containing 100 individuals each were run. Mortality rates and growth in columellar length were evaluated over an experimental period of 135 days. The results showed a clear survival advantage in *T. geversianus* under food deprivation when compared with the other species. This species also showed some growth over the first 45 days of observation. Survival of this species was nearly 90% at 45 days, with mortality increasing at 60 days and about 20% survival present at 105 days, with a few even surviving after 4 months without food. *Chorus giganteus* and *A. monodon* juveniles demonstrated an earlier, continuous mortality, with only 50% survival at 45 days, and 10% survival at 75 days, with none surviving beyond 90 days. There was no increase in size in these juveniles during the study period. The high resistance to fasting in *T. geversianus* juveniles appears due to their high levels of energetic reserves, obtained from high levels of intracapsular extra-embryonic nutrients. This is interpreted as an adaptation to critical seasonal conditions in their natural habitat during their first months of life in the Straits of Magellan.

INTRODUCTION

Benthic marine invertebrates might suffer mortalities of over 90% as juveniles or in their first days of life as they settle into the benthos, as documented by Thorson (1966) in a number of specific cases. More recently, Gosselin and Qian (1997) summarized information on diverse invertebrates, which confirmed an exponential drop in juvenile survival during the first days or weeks post-settlement, with less than 20% survival after four months of life in the benthos. This pattern was also observed by Moran (1999). Attention has been centered on environmental factors, both biotic and abiotic, in determining early mortality in marine organisms as they initiate post-settlement life in the benthos. When mortality factors persist, however, under various environmental conditions, uniformity in mortality of recently settled organisms suggests an intrinsic factor producing a common vulnerability to mortality in these organisms (Gosselin and Qian, 1997). Therefore, some of their structural and functional attributes at the time of settlement need to be ascertained, as these may be included among the factors producing vulnerability in recently settled organisms.

Among these noteworthy intrinsic determinants of vulnerability are their post-settlement size and growth rates upon starting benthic life, as well as the amounts of energy reserves with which they are supplied in this critical stage of their lives. The gradual leveling off of juvenile survival in this early phase is a result of their reaching critical sizes at which their vulnerability to environmental stress is substantially reduced. Unpredictable critical conditions in the environment which may impede these organisms from reaching optimal growth and size for survival may be overcome by the presence of adequate energy reserves in the juveniles at settlement. As a result, evolution has produced initial juvenile sizes and levels of reserves that may be very diverse and varied among species within a given taxon. Thus, embryonic encapsulation, which is characteristic of many marine gastropods, seems to have opened new evolutionary possibilities for the regulation of both optimal sizes of individuals and the nutritional reserves among early juveniles within given cohorts, according to the environmental conditions present in each specific habitat.

Spight's (1976) analysis of data available for muricid snails concluded that probabilities of survival among ju-

veniles increased with growth, where there was an optimal size at hatching determining the corresponding size-specific survival. Selection for larger size at hatching favored survival under environmental stress, reduced problems of dehydration, lowered susceptibility to predation, and provided greater tolerance to temporary conditions of starvation. According to Spight (1976) an optimal hatching size of about 1 mm is prevalent among muricoidean snails with direct development. However, the regularity of this pattern is clearly altered among muricoideans on the coast of Chile, specifically among those at extreme southern latitudes as in the case of the Magellanic species of *Trophon*. These juveniles are between 2.1 to 3.0 mm at hatching (Santana, 1998; Zaixso, 1973), which is more than double the size at hatching and settlement observed in this family as predicted by Spight (1976). This condition is achieved through the unusual mechanism of extra-embryonic feeding on disaggregated nutritive eggs and albuminous fluid during intracapsular development (Penchaszadeh, 1976; Santana, 1998). Microscopic inspection of recently hatched *Trophon* juveniles has shown large relative size (Santana, 1998; Zaixso, 1973) and content of exceptionally high levels of nutritional reserves, indirectly suggesting the potential for survival over long periods of starvation. In order to test this prediction the present study experimentally examined the capacity for survival and growth of *Trophon geversianus* (Pallas, 1769) maintained in the absence of food. The response is compared with parallel observations on two Chilean species in the same family, the snails *Chorus giganteus* (Lesson, 1829) and *Acanthina monodon* (Solander, 1786) whose juveniles, although fed through the typical intracapsular mechanism of provision of nutritive eggs, have a size at hatching of 1 mm, which fits the predicted pattern for snails in this family.

MATERIALS AND METHODS

Origin and Handling of Egg Capsules

Egg capsules of *Chorus giganteus* and *Trophon geversianus* were obtained from adults acclimated in the Marine Culture Center of the Universidad de Los Lagos (CEACIMA) located on Metri Bay (41°36′ S, 72°42′ W). Capsules from *Acanthina monodon* were obtained from the intertidal zone at Mehuin (39°25′ S, 73°13′ W) between July and August 2002.

Once obtained and separated by species, the capsules were placed into culture in the CEACIMA laboratory, Metri, in order to obtain post-hatching juveniles of each species for experimentation. The egg capsules were maintained in a flow-through seawater bath in cylindrical tubes 15 cm in diameter by 20 cm high, having tops, bottoms, and side ports covered with nylon screening (600 μm mesh for *C. giganteus*, *A. monodon*, and 1000 μm mesh for *T. geversianus*). In advanced stages of maturation, the capsules were cleaned manually every week to eliminate fouling and accumulation of sediment.

Experimental Design

Once hatching began, the juveniles obtained were maintained in the containers until the numbers required for the experiments had accumulated. One hundred individuals of each species were selected randomly and deposited into new containers, with three replicates per species. These containers were plastic, with screening both on the walls and over the upper part (top), and arranged in a culture system receiving a constant flow of 30 μm-filtered seawater at about 2 L/min, at ambient seawater temperature. Experimentation was carried out from July 2002 to February 2003. The water temperature in the experimental tanks during the experimental period ranged from 10.5°C (Austral winter) to 11.8°C (spring), reaching a high of 16°C in December and January (summer). The three species were exposed to the same temperature regime in parallel throughout the experiments. In order to comparatively estimate the tolerance of the juvenile snails of the three species to fasting conditions, measurements were made on survival and growth of the individuals. For this, the number and mean size of the hatched individuals of each species were recorded initially. Observations were made every 15 days, recording survival in each replicate and the mean value by species, as well as measuring the size of each individual. The fragile snails were handled with a fine camel-hair brush, fine dissecting forceps, Pasteur pipettes, always within Petri dishes kept on a cold surface so as to reduce any stress due to manipulation and unusual temperature changes. Evidence of mortality was based on the presence of empty shells or shells containing decaying tissue residues. Growth of the snails was determined by measuring the columellar length of each living specimen using an ocular micrometer in a stereoscopic microscope. A daily temperature record was maintained in the laboratory tanks where the experiment took place.

The ideal experimental design for this study would have included a control set of each of the three species of snails maintained under the same conditions as those above, but with abundant food supplies available. In this way, the laboratory-expected mortalities of fed specimens could have been subtracted from those obtained for the fasting specimens. This arrangement was impossible to deploy because of the logistical difficulties in obtaining the large numbers of post-hatching snails required, which included having them in the laboratory in the same season of the year in order to be able to expose the three species to uniform conditions of seawater temperature, oxygen content, photoperiod, and other environmentally dependent factors in the experimental tanks. Based on our previous experience in culturing *C. giganteus*, *A. monodon*, and, more recently, *T. geversianus*, mortalities of fed individuals was low, and we assumed *a priori* that it would not be a factor in the comparative observations among mortalities of the three species in the above described experiment.

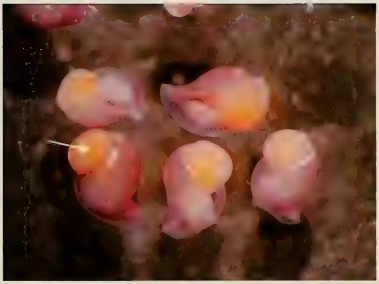

Figure 1. Post-hatching juveniles of *T. geversianus*. Note the important nutrient reserve visible through the apical region of the shell indicated by the arrow.

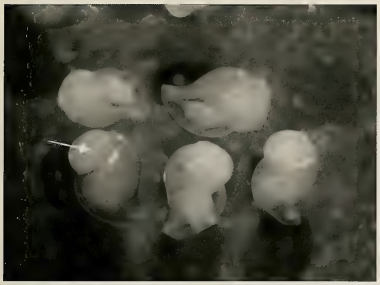

Figure 1. Post-hatching juveniles of *T. geversianus*. Note the important nutrient reserve visible through the apical region of the shell indicated by the arrow.

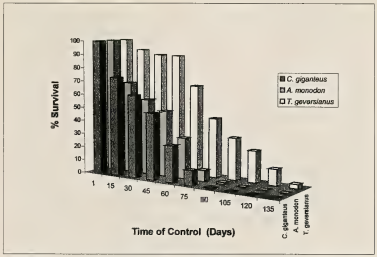

Figure 2. Comparison of survival rates for post-metamorphic juveniles of *C. giganteus*, *A. monodon*, and *T. geversianus* submitted to fasting under experimental conditions over successive time periods.

Statistical Analyses

In order to carry out an analysis of the eventual growth exhibited by the three species, a stage was selected in which the survival was above the population minimum (mean "n"), which could be statistically evaluated as a representative sampling size. In this case, the stage was represented by the first 45 days of the experimental treatment.

Survival and growth in the experimental treatments were examined using analysis of variance (ANOVA; Sokal and Rohlf, 1981). For determination of the significance between differences observed we employed an *a posteriori* Tukey test. All the analyses were carried out using a significance level of 5% ($P < 0.05$). Computer statistical packages for these tests were the SYSTAT 9 ® and Microsoft Excel 97.

RESULTS

Morphological Evidence of Nutritional Reserves in Postmetamorphic Juveniles

A considerable quantity of yolk reserves may be observed through the translucent globose apical region of the shell of post-metamorphic juvenile *T. geversianus* (Figure 1). This material occupies the digestive gland ("hepatopancreas") region, producing a yellow-orange mass visible like large transparent cells. Similar reserves in juveniles of the other species, as observed under the microscope, appear to be markedly smaller than those of the *Trophon*.

Survival Rates during Fasting

Results of the laboratory observations presented in Figure 2 and corresponding analysis of variance, clearly demonstrate the greater tolerance and survival in juveniles of *T. geversianus* under fasting conditions when compared with the data from *C. giganteus* and *A. monodon* under the same experimental treatment. Within *T. geversianus*, the mortality observed in the first 15 day stage was relatively low, at 5–11%; survival continued to be very stable up until day 45. Mortality continued to be more intense and continued to rise after the 2-month measurement. Indeed, at this point the survival was 67% of those starting in the experiment. Over 20% of these snails survived to day 105, and the last few individuals survived fasting past four months of observation.

The *C. giganteus* and *A. monodon* juveniles demonstrated a markedly lower tolerance to fasting, and a parallel relationship, with no significant differences detected by the ANOVA employed among mortality rates throughout the experiment. Beginning with the first 15-day period, the survival of these species was significantly lower than that of *Trophon*, with an intensity that persisted over the subsequent observational periods. There was a greater deterioration in survival capacity in fasting beginning in the early weeks, with no stabilization of mortality as observed in *Trophon* lasting to 45 days. By 45 days, about 50% of both the *C. giganteus* and *A. monodon* populations had died, while at 75 days they showed less than 10% survival. Neither of these species survived past 90 days in the experiment.

Growth Rates

Together with showing comparatively better survival than the other two species during fasting, the *T. geversianus* juveniles also showed significant growth in the sizes of their shells during their period of survival under the experimental conditions (Figure 3). These juveniles, beginning at hatching with a mean columellar length of 2.2 mm, showed a significant increase in length in the ca. 50% of the survivors at 45 days (ANOVA, Table 1). After this period there was no significant growth. In contrast, neither the juveniles of *C. giganteus*, nor those of

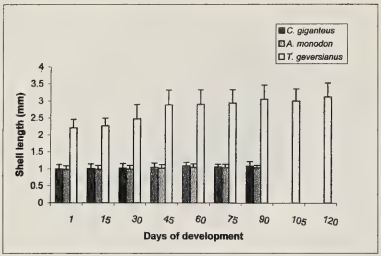

Figure 3. Mean length of post-metamorphic juveniles of *C. giganteus*, *A. monodon*, and *T. geversianus* submitted to experimental fasting over successive time periods.

A. monodon showed any significant shell growth during the time they were maintained without food.

DISCUSSION

The results of the present study clearly confirm the greater viability and survival capacity of post-metamorphic juveniles of *T. geversianus* in absolute absence of food, in comparison with the other two muricids studied. The high resistance to starving allowed high rates of survival for at least two months, with survival declining gradually after this period. To the initiation of this decline may have been added the stress of increased energy expenditure due to the expected rise in the water temperature in December and January. It is possible that within its natural distributional range, the viability of juveniles of *T. geversianus* (attributable to their levels of energy reserves at hatching) may be greater than that shown in our experiments. The high degree of survival of these juveniles is comparable to, or even greater than that reported for newly hatched *Nucella emarginata*, which may survive 50–120 days under fasting conditions (Gosselin and Chia, 1994). This species has extra-embryonic nutrition in the form of nutritive eggs during its embryonic development.

There are at least two properties or attributes in the development of juveniles of *T. geversianus* which may account for its greater resistance to fasting under experimental conditions, including: (a) Large size at hatching of the juveniles (as occurs in *T. geversianus*) which is nearly double that of the other two species, and which is typical of many species in this family (Spight, 1976) and (b) the accumulation of abundant energy reserves due to the existence of a special extra-embryonic nutritive mechanism which maximizes the assignation of raised levels of reserves to each juvenile hatching from the capsules.

Regarding the first attribute, the greater size at hatching of the juveniles of a species, as occurs in *T. geversianus*, increases their relative survival capacity. It is well known that relative body size has a direct metabolic relation to standard metabolic rate in poikilotherms (Peters, 1983; Schmidt-Nielsen, 1984) such that the metabolic cost is greater per unit tissue in smaller organisms than in those of larger size. Spight (1976) noted that an advantageous attribute for survival conferred by larger juvenile size in muricoideans, was that these showed longer periods of resistance to fasting given that in these conditions larger individuals respired less per unit body weight thus prolonging the duration of their nutritional reserves. The size at hatching of *T. geversianus* is among the largest known for the Muricidae, similar only to that of *Murex senegalensis* (with similar numbers of nutritive eggs per embryo) and *Murex angularis* (sensu Knudsen, 1950), although there are no data available on the effects of fasting in these species useful in comparison with present results.

The large accumulation of nutritional reserves observed in the morphological examination of *T. geversianus* post-hatching juveniles is a characteristic of the species that readily distinguishes it from the other species presently studied. This attribute was recognized in previous studies describing the intracapsular development of this species (Zaixso, 1973), and specifically noteworthy is the accumulation of yolk reserves, which can be seen through the apical, translucent sector of the shell. This accumulation allowed characterization of this species as a muricoidean snail whose juveniles had exceptionally high levels of nutritional reserves at the time of their hatching and initiation of life in the benthos. The embryos are provided with abundant food and nutritional reserves prior to hatching by prolonged ingestion of disaggregated yolk in the albuminoid fluid of the egg capsule throughout their long developmental period.

Table 1. Mean size as shell columellar length in postmetamorphic *C. giganteus*, *A. monodon*, and *T. geversianus* subjected to fasting in successive measurement periods. Analysis of variance (ANOVA) is included for growth in length, as well as the index of relative importance (Tukey = 0.05). Not significant at $P > 0.05$; significant at $P < 0.05$.

Time	Length (mm) by species						*ANOVA*		
(days)	*C. giganteus*	n	*A. monodon*	n	*T. geversianus*	n	F	P	Tukey
1	1 ± 0.130	300	0.978 ± 0.110	300	2.209 ± 0.247	300			
15	1.008 ± 0.136	220	0.985 ± 0.117	205	2.264 ± 0.225	278	717.410	0.000	C.g. = A.m. < T.g.
30	1.021 ± 0.134	183	0.992 ± 0.113	169	2.472 ± 0.421	268	9.589	0.014	C.g. = A.m. < T.g.
45	1.049 ± 0.124	147	1.018 ± 0.107	146	2.879 ± 0.434	267	470.929	0.000	C.g. = A.m. < T.g.

Data on intracapsular development of the species (Carcelles, 1947; Zaixso, 1973; Santana, 1998) suggest there are large numbers (900–2000) of nutritive eggs deposited in each capsule that disaggregate at an early stage and become mixed with the albumin to form a nutritive suspension (deutolecital material). About 30 to a maximum of 45 embryos per capsule are fed by this material for an intracapsular period of about four to five months; they measure 2.13 to 3.9 mm at hatching, according to the authors cited above. Thus the embryos may ingest at least 30–50 nutritive eggs each, accompanied by undetermined amounts of the albuminoid mass. This suggests a high degree of nutrient intake which is much greater than that estimated for *C. giganteus* and *A. monodon* with a mean of 10–13 nutritive eggs per embryo (González and Gallardo, 1999; Gallardo, 1979; and recent unpublished data). Uptake of albumin by *T. geversianus* may represent an important nutrient uptake as found by Rivest (1986) for *Urosalpinx cinerea,* the embryos of which, not having nutritive eggs, are fed by the capsular fluid that contains important nutrients in some species (Bayne, 1968; De Mahieu et al., 1974; Bramachary, 1989).

Some specific characteristics of the environment occupied by *T. geversianus* may explain some of the selective pressures that favor its size at hatching and high content of yolk reserves. The high resistance to fasting conferred by these attributes without doubt increases the survivability of these juveniles in situations of limited food availability or in conditions where their access to food is restricted in some way upon initiation of their free-living existence. This may represent selection oriented to maximize early juvenile survival under unfavorable conditions prevalent in the natural habitat occupied by these snails after hatching. This is supported by field observations carried out in the Magellan Straits, which is the normal habitat of the species. Periodic surveys for egg-capsule deposition at low tide in the area have demonstrated the occurrence of an extensive spawning period in spring-summer, with a long intracapsular developmental period that retards hatching of the juveniles to late summer, with most hatching occurring in the fall (Santana, 1998). Thus the first months of life of these juveniles occur during unfavorable fall conditions, and when climatic conditions are extreme during the following winter. Intertidal areas remain exposed at very low temperatures and probably suffer high degrees of desiccation during aerial exposure at low tide.

Although juveniles of *C. giganteus* and *A. monodon* fit the general pattern of many muricoideans by measuring about 1 mm in length, their tolerance to fasting places them at levels that may be considered intermediate to relatively important among the few cases in this family that have been studied (Gosselin and Qian, 1997). The above-cited case of *Nucella emarginata,* whose embryos are also supplied with nutritive eggs, show an important resistance to food deprivation. It should be noted here that muricids having juveniles of similar size (ca. 1 mm) but no provision of extra-embryonic nutrition (e.g. nutritive eggs), survive for very short periods when fasting. In *Urosalpinx cinerea,* for example, the juveniles exhibit direct development without the benefit of nutritive eggs (Spight, 1976), and only survive a week or less in the absence of food (Rittschof et al., 1983). It is very interesting to explore this type of relation with examples from other species inasmuch as this might reveal the possible selective advantages implicated in the evolution of new nutritional strategies for embryos such as nurse egg feeding. Such strategies function in the delicate equilibrium between optimal size at hatching and maximization of the levels of nutrient reserves that the juveniles of different species require for survival of extreme conditions during their early benthic life.

The great similarity shown between juveniles of *C. giganteus* and *A. monodon* relative to survival when fasting is reflected in the similarity between their mechanisms and levels of provision of nutritive eggs during the intracapsular development of their embryos (Gallardo, 1979; González and Gallardo, 1999). Thus, comparison between the intracapsular development of the two species shows a strict similarity indicative of clear differences with the intracapsular conditions shown by other muricids of the region, which supports the hypothesis of a common ancestral origin in the early ontogeny of the two species presently studied (Gallardo, in prep.). The results also support the hypothesis that the levels of nutritional reserves in the juveniles are similar between the two species, explaining their evolution-derived similarity in survival and growth rates under experimental conditions of severe food limitation.

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Euglandina rosea (Férussac, 1821) is found on the ground and in trees in Florida

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Euglandina rosea (Férussac, 1821) is a carnivorous snail native to the southeastern United States, including Florida (Hubricht, 1985; Wolfe and Brooks, 1968). It is known as a ground-dwelling terrestrial snail that feeds on terrestrial gastropods (Burch, 1962; Pilsbry, 1946). Introduced to Hawaii in 1955, it is one of the worst cases of an intended biological control agent attacking nontarget species (Cowie, 2001). Exclosures keep it away from consuming remaining endemic snails, including the endangered *Achatinella* species (Stone, 1999).

On a collecting trip in Marianna, Jackson County, Florida (June 2003), individuals of *E. rosea* were found between 0.3 and 2.0 m above ground on both trees and vines. The majority of individuals were found ~1 m above ground (Figure 1). Collections were made after heavy rains and in high humidity (>80% R.H.—Marianna Airport). Snails were located above the flood plain of the Chipola River. They were found in a clearing within a mixed forest dominated by salt cedar (*Tamarix gallica* L.) and overgrown with vines.

Of the 17 living specimens of *E. rosea* collected, three were found in the leaf litter. Most were found along the trunks of trees or on the underside of leaves. Snails were found immobile either attached with their foot or aestivating, as determined by presence of a mucus epiphragm over their aperture (Burch, 1962). *Euglandina rosea* were found within a 20-m^2 area, coexisting with individuals of the potential prey snails: *Mesodon thyroidus* (Say, 1816), *Stenotrema maxillatum* (Gould, 1848), *Ventridens demissus* (A. Binney, 1843), and *Oligyra orbiculata* Say, 1818. Eggs of *E. rosea* were collected a few centimeters below the surface of the leaf litter.

The literature suggests that *E. rosea* is found primarily in leaf litter (Burch, 1962; Griffiths et al., 1993; Mace et al., 1998; Pilsbry, 1946), although individuals have been known to climb trees or walls to capture prey (Cowie, 2001; Davidson, 1965; Gerlach, 1999; Hadfield et al., 1993; van der Schalie, 1969; Voss, 1976). Davis and Butler (1964) stated that *E. rosea* fed on tree snails in its native habitat. However, these authors did not mention that the introduction of *E. rosea* could threaten native Hawaiian snails. In addition, *E. rosea* is known to

Figure 1. *Euglandina rosea* on vegetation in Marianna, Florida about 1 m above ground. Photograph by DJB.

forage underwater for aquatic snails in Hawaii (Kinzie, 1992).

The behavior of aestivating above ground has serious implications for the use of *E. rosea* as a biological control agent. The ability of *E. rosea* to utilize both trees and leaf litter may allow it to out-compete native species for these resources and allow better access to non-target species (Gerlach, 1999). The use of both ground and tree habitat by *E. rosea* in its native range and aquatic habitat in Hawaii (Kinzie, 1992) makes it a very dangerous species to use in biological control.

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Rediscovery of the syntypes of *Doriopsilla pelseneeri* D'Oliveira, 1895

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The nudibranch mollusk *Doriopsilla pelseneeri* D'Oliveira, 1895, was described by the Portuguese naturalist Paulino D'Oliveira, from Sines (37°57' N, 8°53' W), Portugal, in a paper concerning a number of opisthobranchs from his own collection (D'Oliveira, 1895). There were no illustrations, but the detailed description was sufficient to characterize this distinctive species. In a recent revision of the Atlantic species of the genus *Doriopsilla,* Valdés and Ortea (1997) considered *D. pelseneeri* as a valid name, and redescribed this species adding new relevant morphological, anatomical, and geographical data. Since the type material was untraceable, these authors designated a neotype, collected on May 16, 1992, in Muros de Nalón, northern Spain, and deposited at the Muséum national d'Histoire naturelle (MNHN), Paris, France.

A visit to the Museu Zoológico da Universidade de Coimbra (MZUC), Portugal, after a major reorganization of this institution, made it possible for me to locate Paulino D'Oliveira's opisthobranch collection. It includes five syntypes of *D. pelseneeri* divided into two jars. The larger one contains three specimens (lengths of preserved specimens 20 mm, 20 mm, and 21 mm), the smaller jar contains the remaining two (lengths of preserved specimens 8 mm and 14 mm). Both jars are filled with 70° ethanol. All the specimens bear the same reference number. An old number (160) is still present in a label inside the larger flask, but a new classification of the entire collection of the Museum was implemented in 1945 (Carvalho, 1945), after which both jars were externally labelled with the numeral "20", which corresponds to species number twenty of the "Order Acoela" as stated in the published catalogue (Carvalho, 1945). Hence, the reference number should be indicated as MZUC-Acoela-20.

All specimens are well preserved and certainly were relaxed prior to fixation. The 14 mm specimen has its front partially destroyed, possibly due to the extraction of the buccal bulb. A longitudinal incision between the rhinophores is still visible. The other four remain intact. The color of the preserved specimens is whitish but, drawing from D'Oliveira's description, the animals were reddish or yellow when alive. Recently collected specimens from Sines (personal data) confirm this assumption. As pointed out by Valdés and Ortea (1997), in *D. pelseneeri* the whole mid-portion of the dorsum is covered by large irregular tubercles, a feature that is not present in any other Atlantic species of this genus. These tubercles are easily recognizable in all the syntypes. One of them is illustrated in Figure 1.

According to the fourth edition of the International Code of Zoological Nomenclature (ICZN, 1999), Article 75.8, the rediscovered syntypes automatically become the name-bearing types; the neotype should be set aside. This substitution will cause neither confusion nor instability since the syntypes and neotype belong to the same biological species.

ACKNOWLEDGMENTS

I thank Drs. Isabel Carreira and Rolanda Albuquerque de Matos for the opportunity to examine the types of Paulino D'Oliveira's collection in MZUC. I hold a grant from the *Fundação para a Ciência e Tecnologia,* Portugal (BPD7133/2001). This work was carried out under the scope of the project REN2001-1956-C17-02/GLO (Spanish Ministry of Science and Technology).

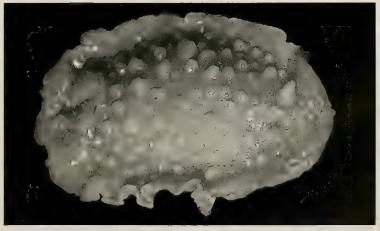

Figure 1. One of the syntypes of *Doriopsilla pelseneeri* D'Oliveira, 1895 (preserved length 20mm).

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CONTENTS

Néstor E. Ardila
Ángel Valdés
The genus *Armina* (Gastropoda: Nudibranchia: Arminidae) in the southern Caribbean, with the description of a new species. . . . 131

Francisco J. García
Jesús S. Troncoso
A new species of the genus *Anetarca* Gosliner, 1991 (Gastropoda: Opistobranchia: Facelinidae) from the western Atlantic Ocean . . . 139

Pilar Carmona Zalvide
Victoriano Urgorri
Francisco J. García
Two new species of *Leptochiton* Gray, 1847 (Polyplacophora) from the Iberian Peninsula (eastern Atlantic coast). . . . 144

Richard Duerr
Cirsotrema (Gastropoda: Ptenoglossa: Epitoniidae) in the Miocene Chipola Formation of northwestern Florida. . . . 152

Geerat J. Vermeij
Greg S. Herbert
A new species of *Stramonita* (Gastropoda: Muricidae) from the Late Pliocene of Florida . . . 157

Luiz R. L. Simone
Diego G. Zelaya
A new *Orbitestella* (Gastropoda: Heterobranchia: Orbitestellidae) from Tierra del Fuego, Argentina. . . . 160

Cristián Ituarte
Sphaeriidae (Bivalvia) from Peruvian Amazon floodplains, with the description of *Pisidium iquito* new species . . . 167

Note

Paul Callomon
Dates of publication of Yochiro Hirase's Kai Chigusa . . . 175

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The genus *Armina* (Gastropoda: Nudibranchia: Arminidae) in the southern Caribbean, with the description of a new species

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ABSTRACT

The southern Caribbean species of the nudibranch genus *Armina* Rafinesque, 1814, are reviewed. *Armina juliana* Ardila and Díaz, 2002, and *Armina muelleri* (Ihering, 1886), two previously described species, are redescribed and their reproductive systems illustrated. The two North American species *Armina abbotti* Thompson, Cattaneo and Wong, 1990, and *Armina wattla* Marcus and Marcus, 1967, are regarded as synonyms of *A. muelleri*, which is reported from the Caribbean for the first time. A new species, *Armina elongata*, is described based on a single specimen collected from Colombia. The number of notal ridges, the size and the shape of the radular teeth, the features of the masticatory processes, and the morphology of reproductive system are the main distinguishing characteristics between the new species and other Atlantic species of *Armina*.

INTRODUCTION

The Arminidae constitutes a poorly known group of living nudibranchs, with nearly 75 described species divided into six genera (Kolb and Wägele, 1998). Arminids are characterized by having an elongated, flattened body, narrower posteriorly, with longitudinal ridges or pustules on the dorsum. The notum bears marginal sacs along its edge. Arminids have a distinct oral veil and retractile rhinophores with a caruncle situated next to them; the radula typically has a broad, denticulated rachidian tooth, and the lateral teeth are falciform (Kolb, 1998). The majority of species in all other genera than *Armina* Rafinesque, 1814 (*Dermatobranchus* van Hasselt, 1824, *Histiomena* Mörch, 1860, *Linguella* de Férussac, 1822, *Pleurophyllidella* Eliot, 1903, and *Pleurophyllidiopsis* Tchang-Si, 1934) are geographically restricted to areas in the Indo-Pacific (Kolb and Wägele, 1998).

Armina is the most species-rich genus of the family, with more than 50 nominal species; it includes the most derived forms of the group (Kolb and Wägele, 1998). Features shared by members of this genus are a continuous anterior mantle margin, the presence of branchial and hyponotal lamellae, and the close distance between the rhinophores. Although *Armina* has a world-wide distribution, only five species have been recorded in the western Atlantic (see Marcus and Marcus, 1960; 1967; Kolb and Wägele, 1998, Ardila and Díaz, 2002).

Armina juliana Ardila and Díaz, 2002, was the only species previously known from the southern Caribbean. The present paper describes two additional species of *Armina* collected from materials trawled off the northern Caribbean coast of Colombia.

MATERIALS AND METHODS

Specimens were collected using a bottom trawl (9×1 m opening, 16 m length) during the cruises INVEMAR-MACROFAUNA I and II, 1999–2001, aboard the R/V Ancón, working off the Caribbean coast of Colombia at depths of 20–500 m. Specimens of Arminidae were sorted and preserved in 70% ethanol. Subsequently, jaws and radulae were dissected and examined using a scanning electron microscope (SEM). The specimens were dissected for study of the reproductive system.

The material examined is deposited at the Museo Nacional de Historia Natural Marina de Colombia, INVEMAR (MHNMC) and the Natural History Museum of Los Angeles County (LACM).

SYSTEMATICS

Family Arminidae Rafinesque, 1814
Genus *Armina* Rafinesque, 1814

Armina juliana Ardila and Díaz, 2002
(Figures 1–2)

Armina juliana Ardila and Díaz, 2002: 27–30, text figs 1–7.

Description: The living animals are bright red with contrasting white longitudinal notal ridges; the anterior

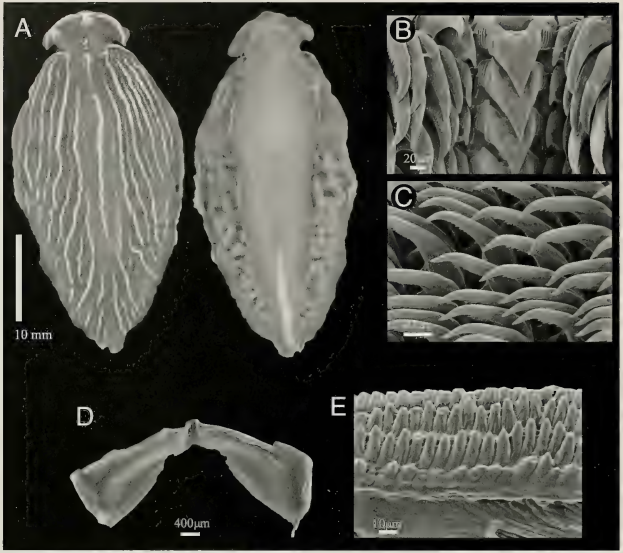

Figure 1. *Armina juliana* Ardila and Díaz, 2002, holotype, MHNMC INV MOL1598. **A.** Dorsal and ventral views of the living animal. **B.** Rachidian teeth. **C.** Lateral teeth. **D.** Jaws. **E.** Detail of the jaw elements on the masticatory processes.

margin of the oral veil and the apical portion of the rhinophores are also white (Figure 1A). Preserved specimens are pale pink. The body is elongated, flattened, narrowing posteriorly. The notum bears 34 longitudinal dorsal ridges, whose margins do not exhibit any black spots of shimmer pigment. The oral veil is small but clearly distinct, with the lateral extension curved backwards and shorter than the widest part of the body (Figure 2A). There are two large club-shaped rhinophores, each one with about 10 vertical lamellae. The rhinophores are situated dorsally on the notum. The eyes are visible through the epidermis at the outer base of each rhinophore. The caruncle is also distinguishable anterior to the rhinophores. The genital opening is located on the right side, anterior to and below the branchial lamellae (Figure 2B). The anal papilla is located slightly behind the midpoint (3/5 of total length, from the anterior end of the body). There are twenty-one branchial lamellae on the right side of the body and nineteen on the left. Fifteen hyponotal lamellae are present on each side of the body. A deep groove is present along the center of the foot sole. The pedal gland is white and located at the posterior end of the foot sole (Figure 1A). Mantle glands (each about 0.7 mm in diameter) are barely distinguishable macroscopically on both sides just behind the branchial lamellae (Ardila and Díaz, 2002).

Jaws and Radula: The radular formula is 27 × 33.1.33 (holotype). The rachidian tooth is broad and bears 12 elongated denticles on each side of the median cusp (Figure 1B). The first lateral tooth is short, bulky and denticulated on the outer side of the cusp. The remaining lateral teeth are elongated and also bear denticles, which become progressively smaller towards the marginal tooth rows. The jaws have a denticulated masticatory border with four rows of denticles (Figures 1D–E).

Reproductive System (Figure 2C): The reproductive system is diaulic. The ampulla is very long, wide and convoluted. The prostate is short and convoluted, composed of two regions: a glandular, proximal region that narrows into the distal, muscular ejaculatory region, which connects directly to the penis. The vagina is short and connected directly to the rounded bursa copulatrix.

Type Material: Holotype (MHNMC INV MOL1598), 41 mm length alive, from type locality; Paratype (LACM 2908), off Palomino, Colombia (11°26′ N, 73°32′ W), 306–312 m depth, muddy bottom, 14 mm length alive.

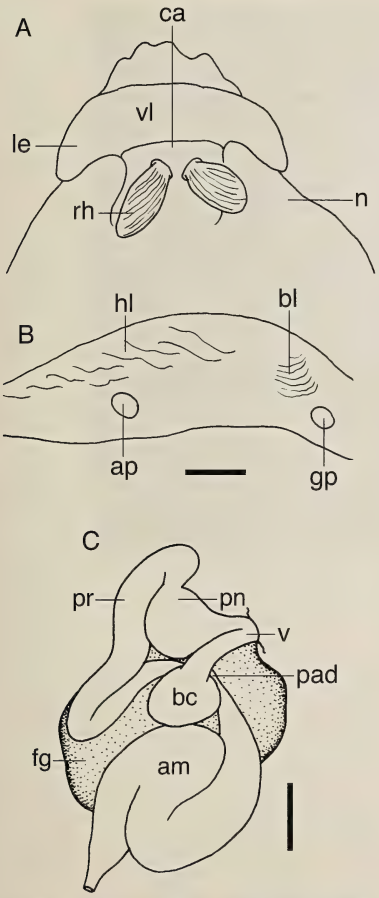

Figure 2. *Armina juliana* Ardila and Díaz, 2002, paratype, LACM 2908. **A.** Dorsal view of the anterior end of the body. Scale bar as in B. **B.** Lateral view of the body. Scale bar = 1 mm. **C.** Reproductive system. Scale bar = 1 mm. Abbreviations: am, ampulla; ap, anal pore; bc, bursa copulatrix; bl, branchial lamellae; ca, caruncule; fg, female glands; gp, genital pore; hl, hyponotal lamellae; le, lateral extension of velum; n, notum; pad, post-ampullary duct; pn, penis; pr, prostate; rh, rhinophore; v, vagina; vl, velum.

Type Locality: Off Cabo de La Vela, Colombia (12°19′ N, 72°42′ W), 460 m depth, muddy bottom.

Distribution: Off Cabo de La Vela and Palomino, Colombia (Ardila and Díaz, 2002).

Remarks: This species was recently described in detail by Ardila and Díaz (2002); a description is repeated here to allow for quick comparisons with the other species treated in this paper. *Armina juliana* can be easily distinguished from other species here described by the position of the genital papilla, which is located anterior to the branchial lamellae, whereas in the other species it is located just posterior to the lamellae. For a comprehensive discussion of *A. juliana* versus other Atlantic species see Ardila and Díaz (2002).

Armina muelleri (Ihering, 1886)
(Figures 3–4)

Pleurophyllidia mülleri Ihering, 1886: 223–228, pl. 9, fig. 1.
Armina abbotti Thompson, Cattaneo and Wong, 1990: 403.
Armina wattla Marcus and Marcus, 1967: 213–216, figs. 16–20.

Description: The animal is red with contrasting yellow longitudinal notal ridges. The anterior margin of the oral veil and the edge of the notum is also yellow (Figure 3A). There are two thin yellow lines surrounding the foot sole and the external edge of the oral tentacles. Preserved specimens are pale grayish. The body is wide, elongated, flattened, with a small notch on the posterior tip. The notum bears 54 longitudinal dorsal ridges, with wider, entire ridges, and thinner, broken ridges intercalated. The oral veil is distinct and has two large, tentacular lateral extensions lacking any projections (Figure 4A). The extensions are as wide as the notum. There are two club-shaped rhinophores, each one with about 30 vertical lamellae. The rhinophores are situated in a notch covered by the anterior end of the notum in the preserved specimens. The eyes are visible through the epidermis at the outer base of each rhinophore. The caruncle is also distinguishable anterior to the rhinophores. The genital opening is located on the right side of the body, slightly posterior to and below the branchial lamellae (Figure 4B). The anal papilla is located behind the midpoint (2/3 of total animal length, from the anterior end of the body). There are 23 branchial lamellae and the same number of hyponotal lamellae on each side of the body. The pedal gland is white and located at the posterior end of the foot sole (Figure 3A). The mantle edge is surrounded by a number of small mantle glands distinguishable macroscopically on both sides.

Jaws and Radula: The radula formula is 36 × 35.1.35 in the single specimen examined. The rachidian tooth is very broad and bears 3–4 large denticles on each side of the median cusp (Figure 3B); the innermost denticle lies very close to median cuspid (Figure 3C). The lateral teeth are elongated and lack denticles (Figure 3D). The jaws have a denticulated masticatory border with four to five rows of denticles (Figures 3E–F).

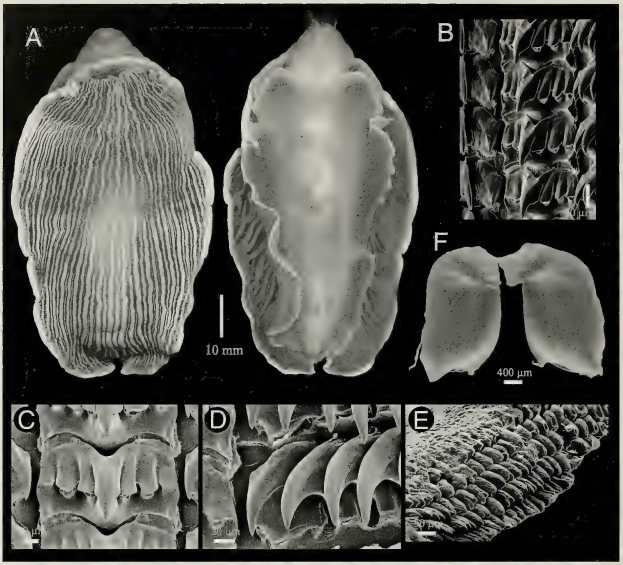

Figure 3. *Armina muelleri* Thompson, Cattaneo and Wong, 1990 (MHNMC INV MOL3901). **A.** Dorsal and ventral views of the living animal. **B.** Rachidian teeth, lateral view. **C.** Rachidian teeth, upper view. **D.** Lateral teeth. **E.** Jaw elements on the masticatory processes. **F.** Jaws.

Reproductive System (Figure 4C–D): The reproductive system is diaulic. The ampulla is very long, wide and convoluted. There is no post-ampullary duct and the ampulla connects directly to the prostate and the female glands. The prostate is very long and convoluted, composed of two regions: a glandular, proximal region that narrows into the distal, muscular ejaculatory region, which connects directly to the penis. The vagina is short, irregular, and connected directly to the rounded bursa copulatrix.

Type Material: Holotype (MHNMC INV MOL3901), 32 mm length alive, from type locality.

Type Locality: Off Salamanca Island, Colombia (11°5′46″ N, 74°40′35″ W), 20 m depth, hard bottom with pennatulaceans (*Renilla reniformis* and *Renilla muelleri*).

Distribution: This species is widespread in the North America and the Caribbean, including records from North Carolina, South Carolina, East Florida, West Florida, Texas, Mexico (Abbott, 1954; Eyster, 1981), and Colombia (present study).

Remarks: *Armina muelleri* was originally described from Brazil by Ihering (1886) as a species with a dark notum covered with light yellow or pale brown ridges. Marcus and Marcus (1960) re-described this species based on specimens much lighter than the type material, but collected from the same area. They argued that intraspecific variation was the cause of differences in color between their material and the original type material. Marcus and Marcus (1960) also conducted the first anatomical examination of this species. The anatomical descriptions by Marcus and Marcus (1960) are very similar to the material here examined. The radula has a rachidian tooth with a central cusp and 3–4 strong denticles on each side, and the reproductive system has a long and convoluted ampulla that connects to an elongate and curved prostate; the vagina is long and straight, connect to an oval bursa copulatrix. Externally, both specimens are also very similar, having a wide and flattened body, with small rhinophores emerging from below the anterior end of the notum, and the genital opening situated slightly posterior to and below the branchial lamellae. The only consistent difference is the absence of denti-

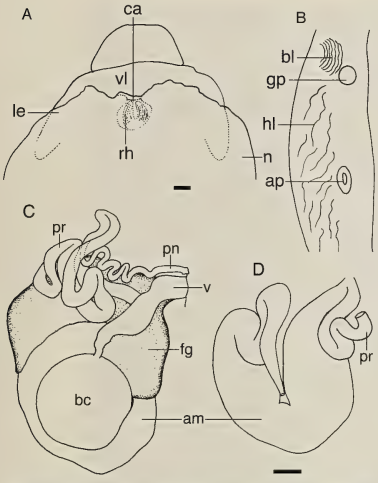

Figure 4. *Armina muelleri* Thompson, Cattaneo and Wong, 1990 (MHNMC INV MOL3901). **A.** Dorsal view of the anterior end of the body. Scale bar = 1mm. **B.** Lateral view of the body. Scale bar as in A. **C.** Reproductive system. Scale bar = 1 mm. **D.** Detail of some reproductive organs. Scale bar as in C. Abbreviations: am, ampulla; ap, anal pore; bc, bursa copulatrix; bl, branchial lamellae; ca, caruncule; fg, female glands; gp, genital pore; hl, hyponotal lamellae; le, lateral extension of velum; n, notum; pad, post-ampullary duct; pn, penis; pr, prostate; rh, rhinophore; v, vagina; vl, velum.

cles on the inner lateral teeth of the Caribbean specimen. Attempts to locate the type material of *Armina muelleri* failed, so the comparisons to our material are solely based on the original description by Ihering (1886), and subsequent re-descriptions by Ihering (1915) and Marcus and Marcus (1960). The absence of denticles on the inner lateral teeth of the Caribbean specimen is probably due to variability within the species, but the possibility that it belongs to an undescribed species cannot be discarded. Since the rest of the anatomy and external morphology are identical to those of *A. muelleri,* the Caribbean specimens is provisionally placed in this species until more material becomes available.

The species name *Armina abbotti* was introduced by Thompson, Cattaneo and Wong (1990) for the North American specimens identified by Abbott (1954) and Eyster (1981) as *Armina tigrina* Rafinesque, 1814. The publication of the name is accompanied by bibliographic references to descriptions and therefore it meets the requirements of the International Code of Zoological Nomenclature, ICZN (1999: Article 13.1.2). Examination of the descriptions of specimens of *A. tigrina* in the papers of Abbott (1954) and Eyster (1981), and the original description of *Armina muelleri* and subsequent re-descriptions by Ihering (1915) and Marcus and Marcus (1960) revealed that the external morphology and anatomy of all these specimens are virtually identical, and there is no doubt they belong to the same species. Again, the type material of *Armina abbotti* is untraceable, so comparisons are based on the literature available. The radula of the material studied by Eyster (1981) from South Carolina has a rachidian tooth with a central cusp and 4 strong denticles on each side, and the inner lateral teeth bear some denticles, very similar to those of the specimens from Brazil. The illustrations of the living animals by Eyster (1981) show a species with a broad velum and the rhinophores emerging ventrally to the anterior end of the notum.

Nijssen-Meyer (1965) described one specimen of *Armina* from Surinam that he identified as belonging to the tropical Indo-Pacific species *Armina semperi* (Bergh, 1861). This identification was based on the fact that the specimen from Surinam had more rows of denticles in the masticatory process than specimens of *Armina muelleri* and the innermost lateral teeth had numerous denticles instead of a few or none. These differences in the number of rows seem to be due to intraspecific variation. The external morphology and the shape of the rachidian tooth and the lateral teeth of the Surinam material are identical to those of other references to *A. muelleri* (Ihering, 1915; Marcus and Marcus, 1960). Thus the specimen described by Nijssen-Meyer (1965) is here regarded as *A. muelleri,* concurring with the earlier suggestion by Marcus and Marcus (1967).

A third species name introduced for the Western Atlantic is *Armina wattla* Marcus and Marcus (1967), originally described from Georgia, USA. This species is also similar to *Armina muelleri* in radular and reproductive morphology. Both species have wide rachidian teeth with a few strong denticles on each side of the cusp and innermost denticulate lateral teeth. The reproductive only differs in the more elongate vagina of *A. wattla*; we assume that the elongate duct interpreted by Marcus and Marcus (1967) as the albumen gland is actually the ampulla. Externally, *A. wattla* is similar to *A. muelleri* by having a wide and flattened body, lamellated rhinophores emerging from below the anterior border of the notum, and the genital opening situated posterior to and below the branchial lamellae. Marcus and Marcus (1967) argued that *A. wattla* differs from *A. muelleri* by the shape of the caruncule (with two lobes in the former) and the size of the radular teeth. However, examination of the re-description of *A. muelleri* by Marcus and Marcus (1967) shows no significant differences in the shape of the caruncle.

Because of the absence of consistent and distinctive differences, we regard *A. wattla* and *A. abbotti* as junior synonyms of *A. muelleri.*

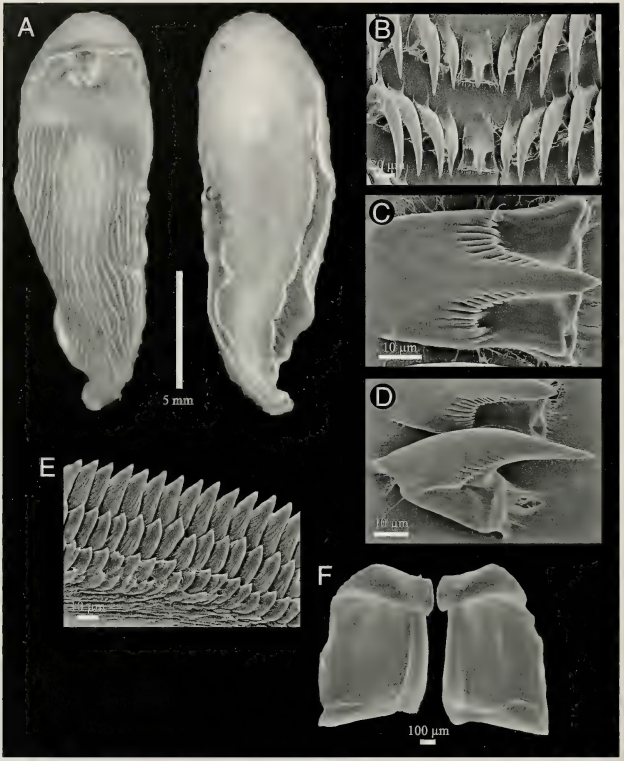

Figure 5. *Armina elongata* new species, holotype, MHNMC INV MOL3902. **A.** Dorsal and ventral views of the living animal. **B.** Rachidian teeth and inner lateral teeth. **C.** Detail of the rachidian tooth. **D.** Detail of the innermost lateral tooth. **E.** Jaw elements on the masticatory processes. **F.** Jaws.

Armina elongata new species
(Figures 5–6)

Description: The living animal is red with white longitudinal notal ridges. The anterior margin of the oral veil and the apical portion of the rhinophores are also white (Figure 5A). The preserved specimen is pale grayish, almost white, with the spaces between the longitudinal notal ridges pigmented with dark gray. The body is elongated, flattened, and narrower posteriorly. The notum bears 24 longitudinal dorsal ridges. The oral veil is distinct and has two large, tentacular lateral extensions without any projections. The extensions are as wide as the notum. There are two club-shaped rhinophores, each one with about 20 vertical lamellae situated on a dorsal notch. The eyes are visible through the epidermis at the outer base of each rhinophore. The caruncle is also distinguishable anterior to the rhinophores. The genital opening is located on the right side, slightly posterior to and below the branchial lamellae. The anal papilla is located behind the midpoint (2/3 of total animal length, from the anterior end of the body). There are 22 branchial lamellae and 23 large hyponotal lamellae on each side of the body. The branchial and hyponotal

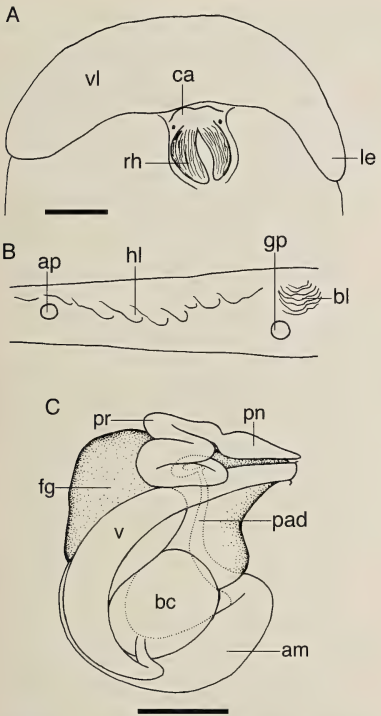

Figure 6. *Armina elongata* new species, holotype, MHNMC INV MOL3902. **A.** Dorsal view of the anterior end of the body. Scale bar = 1mm. **B.** Lateral view of the body. Scale bar as in A. **C.** Reproductive system. Scale bar = 1 mm. Abbreviations: am, ampulla; ap, anal pore; bc, bursa copulatrix; bl, branchial lamellae; ca, caruncule; fg, female glands; gp, genital pore; hl, hyponotal lamellae; le, lateral extension of velum; n, notum; pad, post-ampullary duct; pn, penis; pr, prostate; rh, rhinophore; v, vagina; vl, velum.

lamellae show alternation of larger and smaller lamellae. The pedal gland is white and located at the posterior end of the foot sole (Figure 5A).

Jaws and Radula: The radula formula is 26 × 33.1.33 in the holotype. The rachidian tooth is narrow, with a long and pointed median cusp, and bears approximately 20 thin and elongated denticles on either side of the median cusp (Figure 5C). The lateral teeth are elongated, curved and also bear denticles that become progressively smaller towards the outermost teeth. The jaws have a denticulated masticatory border with three to four rows of denticles (Figures 5E–F).

Reproductive System (Figure 6): The reproductive system is diaulic. The ampulla is large and convoluted; it narrows into a long post-ampullary duct that connects to the prostate and the female glands. The prostate is short and convoluted, and connects directly to the penis. The vagina is very long, curved and connected directly to the rounded bursa copulatrix.

Type Material: Holotype (MHNMC INV MOL3902), length 16 mm alive, from type locality.

Type Locality: Off Manaure, Colombia (11°53′5″ N, 72°36′39″ W), 22 m depth, substratum with coralline algae and gravel.

Distribution: This species is only known from the type locality, off Manaure, Colombia.

Etymology: The specific name refers to the elongate shape of the body and the masticatory processes of this species.

Remarks: *Armina elongata* is clearly distinguishable from other species of the genus in several regards. Externally, the body shape of *A. elongata* is proportionally longer and narrower than that of *A. juliana* or *A. muelleri.* The velum is much wider than that of *A. juliana* and as wide as the notum. The genital opening is situated posterior to the branchial lamellae, whereas in *A. juliana* is anterior to the branchial lamellae.

Other differences include the reproductive system and the radular morphology. *Armina elongata* has a much more elongated vagina than those of *A. juliana* and *A. muelleri.* The rachidian tooth of *A. elongata* is most similar to that of *A. juliana,* but the central cusp is sharper and more elongated and has more denticles, almost reaching the apex of the cusp.

The description of *A. elongata* constitutes the second record of the genus *Armina* and the family Arminidae in the Caribbean Sea after the original description of *A. juliana* (see Ardila and Díaz, 2002). Additionally, this is the third arminid known to occur in the western Atlantic with *A. juliana* and *A. muelleri* (see Kolb and Wägele, 1998 and Ardila and Díaz, 2002).

DISCUSSION

Comparisons of the external morphology and anatomy of *Armina elongata, A. muelleri,* and *A. juliana,* examined in this study, reveal that they are easily distinguishable from each other and from other Atlantic species of the genus by at least one or more external characters. The numbers of branchial and hyponotal lamellae, which vary little within the southern Caribbean species, show a great variation among other Atlantic species, and in some cases the number of lamellae differs from side to side. *Armina tigrina* has the largest number of branchial

lamellae (more than 100 per side), whereas *A. maculata* has the largest number of hyponotal lamellae (more than 100 per side). For other Atlantic species, *Armina neapolitana* has 18–32 branchial lamellae and 9–19 hyponotal lamellae, and *Armina loveni* has 9–26 branchial lamellae and 15–25 hyponotal lamellae (see Kolb, 1998). *Armina wattla* has 28 branchial leaves and more than 29 lateral lamellae when all primordial are counted (Marcus and Marcus, 1967).

The shape of the radular teeth, which appears to show little intraspecific variability in arminids (Marcus and Marcus, 1966), is another useful set of characters to distinguish species (see Kolb, 1998 and Ardila and Díaz, 2002). Several species have a distinct innermost lateral tooth, frequently bearing small denticles on the sides of the cusp, whereas the other lateral teeth have elongate cusps that can be denticulated or smooth. However, the material of *Armina muelleri* here examined lacks denticles on the innermost lateral teeth, which are present in other specimens described in the literature. However, other anatomical similarities suggest that this variation in the presence of denticles is likely due to intraspecific variability. Distinctive radular formulae and rachidian teeth morphology are found in other Atlantic species of the genus. In *A. tigrina* the radular formula is 35 × 56.1.56 and the central cusp of the rachidian tooth is not as broad as in *A. juliana* and *A. muelleri* and bears 15–18 fine denticles. In *A. loveni* the radular formula is 35 × 29.1.29 and the rachidian tooth has five coarse denticles on each side.

Finally, the morphology of the reproductive system has provided useful information to distinguish the three species here examined. In *A. elongata* the vagina is very long, curved and the ampulla is large and narrows into a long post-ampullary duct that connects to the prostate, whereas in *A. muelleri* the vagina is short and there is no post-ampullary duct connecting the ampulla directly to the prostate, which is very long and convoluted. *Armina juliana* also has a post-ampullary duct, but the vagina is much shorter than in the other two species.

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A new species of the genus *Anetarca* Gosliner, 1991 (Gastropoda: Opistobranchia: Facelinidae) from the western Atlantic Ocean

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ABSTRACT

The genus *Anetarca* Gosliner, 1991, has been known as monotypic, with *A. armata* Gosliner, 1991, described from the Pacific coast of North America, as its type species. In this paper, a second species of the genus, *Anetarca brasiliana* new species, is described from the locality of Búzios, State of Rio de Janeiro (Brazil). It constitutes the first species of the genus found in the western Atlantic Ocean. The distinguishing characters of this species are the color pattern, the presence of lamellate rhinophores, and the penial duct provided with an apical elongate appendage.

INTRODUCTION

In 1991, Gosliner described the genus *Anetarca,* with the type species *A. armata,* belonging to the family Facelinidae, from the Pacific coast of central Baja California. The present paper describes a new species of *Anetarca* collected in Búzios (State of Rio de Janeiro, Brazil). It thus constitutes the second known species of that genus and the first species found in the Atlantic Ocean. MNCN stands for Nacional de Ciencias Naturales de Madrid, Spain, and MORG stands for Museu Oceanográfico "Prof. Eliézer de Carvalho Rios", Fundação Universidade do Rio Grande, Rio Grande, Brazil.

SYSTEMATICS

Genus *Anetarca* Gosliner, 1991

Anetarca brasiliana new species
(Figures 1–7)

Description:

External Anatomy (Figures 1–3): Body elongated. Foot broad and with elongated propodial tentacles. Rhinophores long, with 7–10 lamellae obliquely arranged. Lamellae connected by a longitudinal ridge on anterior and posterior faces of rhinophores. Rhinophores join at their bases. Eyes located behind bases of rhinophores. Oral tentacles considerably long, their length approximately half body size. Cerata cylindrical and slightly curved, cnidosac pointed. Precardiac cerata forming an arch containing a single row of cerata. Postcardiac cerata arranged in 9 clusters, each containing only a single row. Number of cerata per cluster in 7.5 mm specimen is: one precardiac arch with seven cerata and nine postcardiac rows with 4, 4, 4, 4, 3, 3, 2, 1, 1 cerata, respectively. Gonopore ventral to precardiac ceratal arch. Anus cleioproct, situated between first two postcardiac ceratal rows.

Coloration: General body and foot color translucent orange-brown with numerous white spots more or less densely concentrated, giving appearance of transverse white bands along dorsal surface of notum. Rhinophores and oral tentacles have same general color pattern, although apical third of rhinophores is almost translucent white, while on basal two-thirds orange-brown is more intense. In this portion borders of lamellae are red. Cerata have same superficial color pattern as body, with translucent-white cnidosac and dark-brown digestive diverticulum. Jaws visible externally and rose colored.

Internal Anatomy (Figures 4–11): Buccal apparatus with a series of oral glands on dorsal and lateral surfaces of its oral tube. Jaws rose colored, having a rather short masticatory border with irregular denticles (Figures 5, 8, 9). Radular formula in two of specimens, 7.5 and 8 mm long, is 12 × 0.1.0 and 16 × 0.1.0, respectively. Teeth arch-shaped, with broad and elongate central cusp and 9–11 elongate denticles on either side of cusp. Lateral denticles decrease in size toward margins (Figures 10, 11).

Reproductive System (Figures 6, 7): With narrow preampullar hermaphroditic duct. Duct connected to a broad and curved ampulla, which divides into a short oviduct and a narrow and coiled deferent duct. Oviduct

Figure 1. *Anetarca brasiliana.* Living holotype, MORG 40608, 9 mm length.

with a small seminal receptacle located anteriorly to junction with female gland mass. Deferent duct lacks a differentiated prostate. Penial papilla broad and curved. Penial duct shows narrow prolongation at its tip and a subterminal, curved and elongated chitinous stylet (Figure 7).

Biological Notes: When the animals are disturbed, the rhinophores bend forward and touch, crossing each another. In addition, the oral tentacles curve backward, bending around the rhinophores; the cephalic and precardiac region of the body move upwards. This display disappears when the molesting stimulus is removed.

Holotype: MORG 40608, 9 mm length, Francisco J. García and Jesús S. Troncoso colls., 24 Mar. 1998.

Paratypes: MORG 40609, paratype 1, from type locality, 6 mm length; MNCN 15.05/33182, paratypes 2 and 3, Praia dos Ossos, Armação dos Búzios, Brazil, 4 and 4.5 mm length respectively, Francisco J. García and Jesús S. Troncoso colls, 26 Mar. 1998.

Type Locality: Collected in the intertidal zone at Praia da Armação, Armação dos Búzios (State of Rio de Janeiro, Brazil).

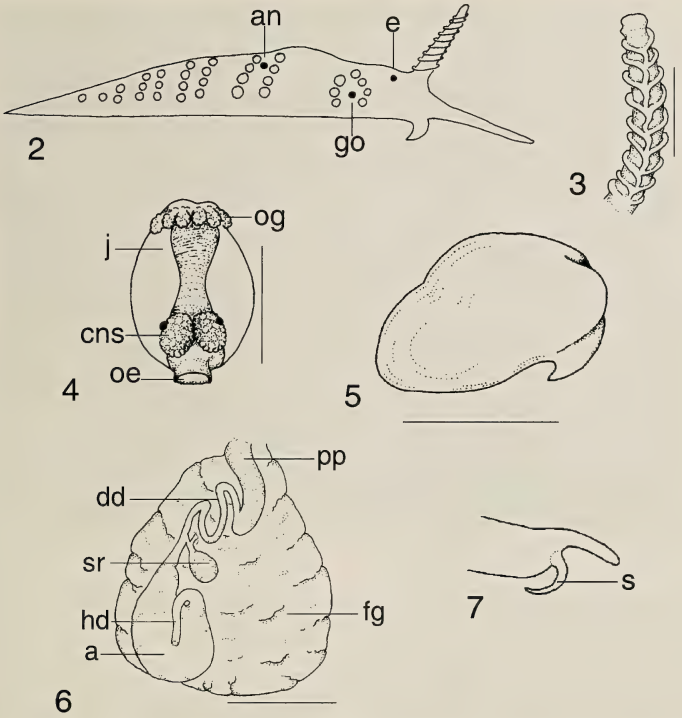
Other Material Examined: Two specimens, 7.5 and 8 mm in length, were collected in the intertidal zone at Praia da Armação, Armação dos Búzios (State of Rio de Janeiro, Brazil) (24 Mar. 1998), Francisco J. García and Jesús S. Troncoso colls.

Etymology: The name of this species, *brasiliana,* is dedicated to Brazil, the country where the specimens were collected.

DISCUSSION

Brazilian opisthobranchs and those from other western Atlantic areas were intensely studied for more than thirty years by Ernst and Eveline Marcus. However, the tropical western Atlantic opisthobranch fauna is not as well known as the Indo-Pacific fauna (Millen and Hamann, 1992) and that from the eastern Atlantic. Marcus (1977) published a checklist of the warm-water opisthobranchs found from La Plata (Argentina) to Cape Hatteras (USA), in which, eleven species of the family Facelinidae were cited. Posteriorly, Millen and Hamann (1992) described another species of this family from the Caribbean Sea, *Pauleo jubatus* Millen and Hamann, 1992. García and Troncoso recently (2003) named a species of *Phidiana* from Archipelago Fernando de Noronha (off northeastern Brazil). Eight species of Facelinidae have been cited from Brazilian waters, *Phydiana lynceus* Bergh, 1867, *Facelina coenda* Marcus, 1958, *Cratena pilata* (Gould, 1870), *Dondice occidentalis* (Engel, 1925), *Godiva rubrolineata* Edmunds, 1964, *Nanuca sebastiani* Marcus, 1957, *Favorinus auritulus* Marcus, 1955 (Marcus, 1977; Rios, 1994) and *Phidiana riosi* García and Troncoso, 2003.

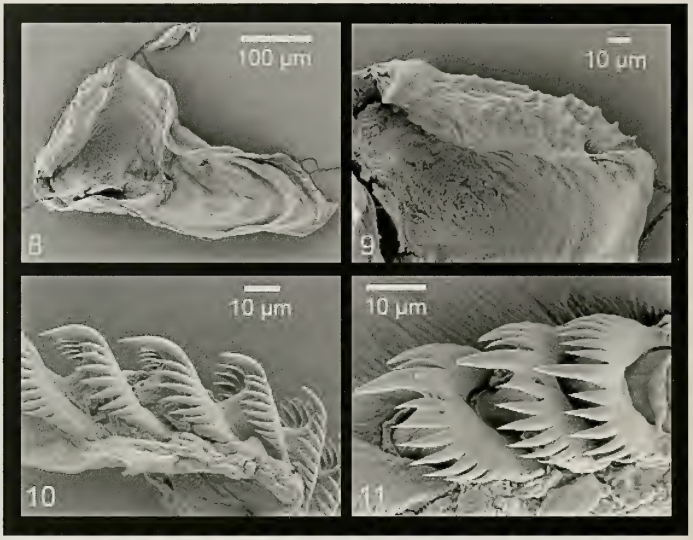
The species described in this paper differs externally from other facelinid species by the coloration and arrangement of cerata. In *Phydiana lynceus, Phydiana riosi,* and *Facelina. coenda* all cerata are arranged in rows (Marcus, 1958; Edmunds and Just, 1983; García and Troncoso, 2003); in *Dondice occidentalis* and *Godiva rubrolineata* the cerata are arranged in arches with more than one row of cerata per arch (Marcus, 1958; Edmunds, 1964); *Nanuca sebastiani* has only four groups



Figures 2–7. *Anetarca brasiliana.* **2.** Diagrammatic right profile showing the insertion of the cerata and position of the anus and reproductive apertures. **3.** Rhinophore. **4.** Dorsal view of the buccal apparatus. **5.** Jaw. **6.** Reproductive system. **7.** Detail of the penial duct. Abbreviations: a, ampulla; an, anus; cns, central nervous system; e, eye; dd, deferent duct; fg, female gland; go, genital opening; hd, hermaphroditic duct; j, jaw; oe, oesophagus; og, oral glands; pp, penial papilla; s, stylet; sr, seminal receptacle. Scale lines = 0.5 mm.

of cerata arising from a transversely set base (Marcus, 1957; Edmunds and Just, 1983); in *F. auritulus* the cerata are arranged in arches (Edmunds and Just, 1983) or the two first groups of cerata are arched and the hinder groups form simple rows (Marcus, 1955); finally, *Cratena pilata* has the first three groups arched and the three hinder ones forming oblique rows (Marcus, 1957). In addition, the rhinophores of our species differ from those of *F. auritulus* and *C. pilata.* In *F. auritulus,* the rhinophores are smooth and bear two bulbs (Marcus, 1955; Edmunds and Just, 1983); in *C. pilata* they are either covered with small tubercles (Marcus, 1957) or smooth (Marcus and Marcus, 1967). The penis is unarmed in all the Brazilian facelinid species except for *P. lynceus, P. riosi,* and *F. coenda. Phidiana lynceus* and *P. riosi* have a hook-shaped penial stylet (Marcus and Marcus, 1967; García and Troncoso, 2003) and in *F. coenda* the border of the penial leaf bears small protuberances prolonged into one to four brown spines (Marcus, 1958).

There are six other species of Facelinidae from the warm western Atlantic waters, *Palisa kristenseni* (Marcus, 1963), *P. papillata* Edmunds, 1964, *Learchis poica*



Figures 8–11. *Anetarca brasiliana.* Scanning electron micrographs. **8.** Jaw. **9.** Masticatory border. **10–11.** Radular teeth.

Marcus, 1960, *L. evelinae* Edmunds and Just, 1983, *Austraeolis catina* Marcus and Marcus, 1967, and *Pauleo jubatus* Millen and Hamann, 1992. Our species differs from both species of *Palisa* because in these species the rhinophores are covered with papillae, the radular teeth lack a prominent central cusp, and the penis is unarmed (Edmunds, 1964; Marcus and Marcus, 1970). *Austraeolis catina* has the three anterior groups of cerata arched and its penis ends on a disc whose edge is beset with ten broad warts, each bearing a tiny spine; there are two additional warts on the surface of the disc, also with spines (Marcus and Marcus, 1967). *Pauleo jubatus* differs from our species by the arrangement of the cerata groups in arches, the shape of the radular teeth, and the presence of a penial sac (Millen and Hamann, 1992). In the species of the genus *Learchis,* the post-pericardial groups of cerata are arched while the pre-pericardial ones form oblique rows; the penis is unarmed (Edmunds, 1964; Marcus and Marcus, 1970; Edmunds and Just, 1983).

Learchis poica Marcus and Marcus, 1960, is a variable Caribbean species. However, there are several anatomical features that allow us to differ *L. poica* from our specimens.

Learchis poica has the precardiac cerata arranged in 5–6 rows, and the postcardiac cerata form 6–7 arches (Marcus and Marcus, 1960; Edmunds and Just, 1983). In *Anetarca brasiliana* new species, the precardiac cerata form one arch and the postcardiac are arranged in 9 rows. The radular teeth of *L. poica* have a prominent cusp flanked by 5–8 denticles (Marcus and Marcus, 1960), while in *A. brasiliana* the radular teeth have 9–11 lateral denticles on each side of the central cusp. In addition, the deferent duct in *L. poica* is divided into a proximal narrow, not-glandular portion and a wide prostatic region that continues within the blunt penis (Marcus and Marcus, 1960); in *A. brasiliana* there is not a differentiated prostatic region of the vas deferent.

We have allocated the new species in the genus *Anetarca* Gosliner, 1991, because of the arrangement of cerata, with a pre-anal arch and single postanal rows, the shape of the radular teeth with a prominent central cusp, the male ducts lack a penial gland and the penis has a subterminal and curved penial spine.

Our specimens coincide with *Anetarca* in the features that characterize that genus, except the rhinophores, because in *A. armata* (the type species) the rhinophores are smooth while in our species they have oblique lamellae. Thus, we suggest that it should be allocated in the genus *Anetarca,* and that the generic definition be expanded to include species with smooth or lamellate rhinophores. A similar situation occurs in genus *Flabel-*

lina (Flabellinidae), which includes species with smooth, or ringed (annulate or perfoliate), or papillate rhinophores (Gosliner and Griffiths, 1981; Gosliner and Willan, 1991).

In addition to the ornamentation of the rhinophores, *A. brasiliana* differs externally from *A. armata* because in the former the oral tentacles are clearly longer than the rhinophores, while in *A. armata* they are shorter. Internally, *A. brasiliana* has the masticatory border of the jaws denticulated and the penial duct having an elongated apical appendage.

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Two new species of *Leptochiton* Gray, 1847 (Polyplacophora) from the Iberian Peninsula (eastern Atlantic coast)

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ABSTRACT

Two new species of the genus *Leptochiton* (Polyplacophora) from the Atlantic Ocean are described: *Leptochiton* (*Leptochiton*) *troncosoi* and *Leptochiton* (*Leptochiton*) *pepezamorai* were collected off Spain at 753–832 m depth. Both species have been included in genus *Leptochiton*, subgenus *Leptochiton*, due to the presence of thin valves without insertion plates, tegmentum finely granulated with granules of equal size, and the dorsal girdle covered with small scales. The new species are characterized by their elongate-oval shape, tegmentum sculptured with thin rounded granules, which tend to form strings, and girdle dorsally covered with long, non-imbricate scales. The larger lateral tooth of the radula is bicuspid in *L.* (*L.*) *troncosoi*, and unicuspid in *L.* (*L.*) *pepezamorai*. Among all the known species of *Leptochiton*, the new species are more similar to *L.* (*L.*) *xanthus*, *L.* (*L.*) *tenuis*, *L.* (*L.*) *geronensis* and *L.* (*L.*) *thalattius*. In this paper the anatomic features of the new species are compared with all the species of *Leptochiton*.

INTRODUCTION

The species of the genus *Leptochiton* Gray, 1847, have been revised by Kaas (1979, 1981, 1991), Van Belle (1983), Kaas and Van Belle (1985, 1987, 1990, 1994), Dell'Angelo and Palazzi (1991, 1986, 1987), Della Bella and Dell'Angelo (1985), Cesari (1987), and Carmona and Urgorri (1999). These studies allow us to determine the actual worldwide diversity of *Leptochiton*. Nevertheless, some specimens collected off northwestern Spain have features that differ from those of the species described in these previous works. We describe herein, using light and scanning electron microscopes, two new species of *Leptochiton* based on their distinctive shell, radula, and girdle scales.

MATERIALS AND METHODS

The specimens were collected in 1990–1991 during the "Cangrexo I" campaign off A Quiniela (Galicia, northwestern Spain) between 753–832 m depth. The specimens were collected using royal crab (*Chaeceon affinis*) traps. They were preserved in 70% ethanol. To study the hard parts (shells, scales, girdle spicules, and radulae) the animals were macerated in 10% KOH and rinsed with distilled water. For SEM (Philips XL-20), shells, radulae, and girdle scales were coated with gold. MNCN stands for Museo Nacional de Ciencias Naturales, Madrid, Spain.

SYSTEMATICS

Class Polyplacophora Gray, 1821
Order Neoloricata Bergenhayn, 1955
Suborder Lepidopleurina Thiele, 1910
Family Leptochitonidae Dall, 1889
Genus *Leptochiton* Gray, 1847 (Type species: *Chiton cinereus* Montagu, 1803, non Linnaeus, 1767).

Diagnosis: Valves thin, lacking insertion plates and tegmentum finely granulated. The granules are of equal size and the girdle is dorsally covered with small scales.

Leptochiton (*Leptochiton*) *troncosoi* new species
(Figures 1–20)

Diagnosis: Elongate-oval shape, twice as long as wide, moderately elevated, the back is evenly rounded and with a marked apex. The color of tegmentum is dark beige. The tegmentum is sculptured with thin rounded granules that tend to form strings among which semicircular and concentric growth lines of the shell are shown. The girdle is narrow, covered with long non-imbricate scales. The major lateral tooth of the radula is bicuspid, and the internal cusp is small.

Description: The head valve has a semicircular anterior border whereas the posterior valve forms such a blunt angle that it hides the notch of the concave apex. The strong slope originated at the head valve is convex (Figure 1). The intermediate valves have rectangular borders except for the second valve, whose anterior mar-

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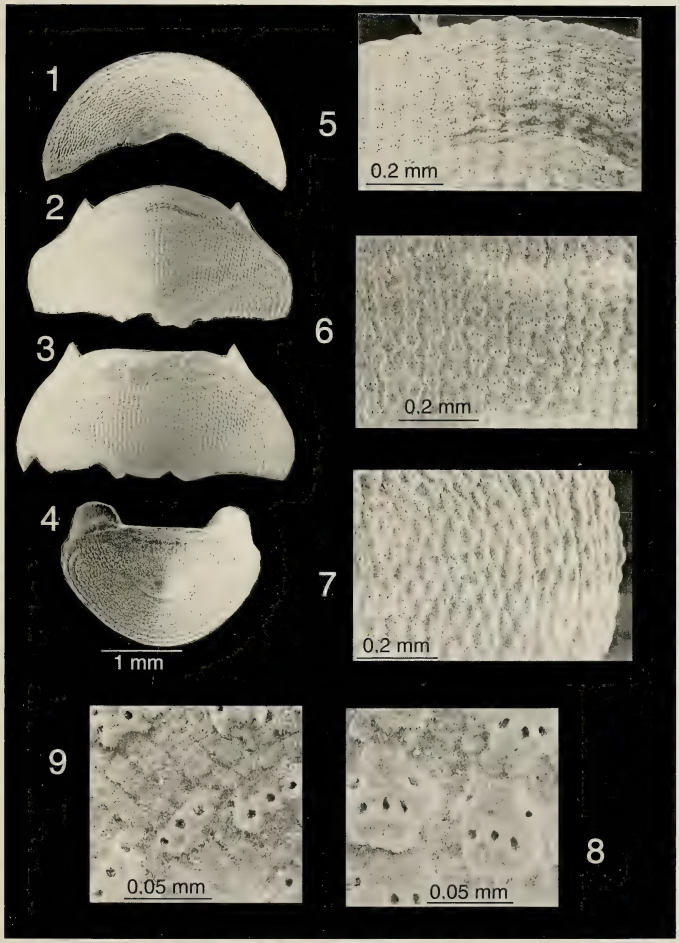
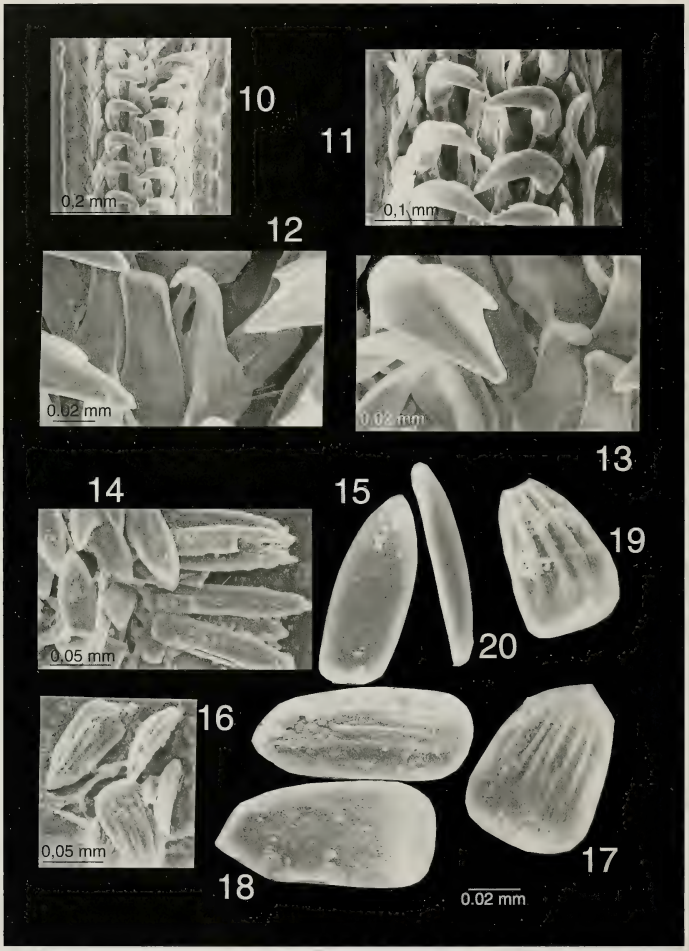


Figures 1–9. *Leptochiton (L.) troncosoi.* **1.** Valve I. **2.** Valve II. **3.** Valve IV. **4.** Valve VIII. **5.** Arrangement of granules on jugal area. **6.** Arrangement of granules on pleural area. **7.** Arrangement of granules on lateral area. **8.** Arrangement of megalaesthetes and micraesthetes on central area of the granules. **9.** Arrangement of megalaesthetes and micraesthetes on lateral area of the granules.



Figures 10–20. *Leptochiton* (*L.*) *troncosoi*. **10–11.** Radula. **12.** Central and first lateral radular teeth. **13.** Cusp of the major lateral tooth and spatulate uncinal tooth. **14.** Arrangement of ventral scales and marginal spicules. **15.** Ventral scales. **16.** Arrangement of dorsal scale. **17.** Dorsal scale, dorsal view. **18.** Dorsal scale, ventral view. **19.** Dorsal corpuscle. **20.** Marginal spicules.

gin is completely convex (Figures 2, 3). However, in the remainder of valves it tends to be convex although it may be slightly concave in the jugal sinus. The lateral borders are rounded while the posterior borders are straight; they converge on the apex, and a little concave curvature is noticeable on both sides. The lateral areas are not raised, but are only visible on the sculpture. The tail valve is smaller in size than the head valve. The anterior margin of the caudal valve is similar to the intermediate valves and the semicircular posterior border. It has a prominent mucro at an antero-central position, which forms a strong slope (Figure 4).

The tegmentum has rounded granules forming a stem-like sculpture. The granules form parallel longitudinal strings in the central area (Figure 2). The granules are wider and flattened in the jugal area, and exhibit an apical stem divided into three parts that are usually connected to the next granule (Figure 6). On the pleural area, the granules are longer and the stems are smooth. The number of strings on the central area may be between 63 and 67 in the intermediate valves. At the head valve, lateral areas, and postmucral area, the strings are radially oriented (Figures 1, 2, 3, 4). The granules on both terminal valves are rounded with no stems (Figure 5), while on the lateral areas the shape is wider (Figure 7); arranged on a radially striate tegmentum, three striations are found on each granule. Eighty-nine strings are observed on the head valve, 58 on the tail valve, and 11–14 on the lateral areas.

The aesthetes are arranged in groups of five on each granule, although sometimes only three aesthetes may be seen (Figures 8, 9). They are situated at the edges of the granules except for the central one, which is located in a subcentral position on the granule.

The articulamentum is white, has fragile appearance, and lacks insertion plates. The apophyses are widely separated by the large jugal sinus. It has triangular shape on the intermediate valves and is trapezoid with rounded edges on the tail valve.

The dorsal girdle is covered with slightly convex, elongate, curved, pointed scales, up to 90 × 53 μm each (Figure 16). They are sculptured with about 5–8 longitudinal ribs (Figures 17–19). Along the marginal there is a fringe of stronger cylindrical spicules up to 200 μm in length (Figure 14). Ventrally the girdle is lined with triangular scales of 20–28 μm; scales become more elongate (70–120 μm) and weakly ribbed toward the outer margin.

The gills are arranged in rows at both sides of the foot. They are inserted at the level of valve VII, extend to the anus with a gradual increase in size, but size decreases at the last valve. Thus, the gills are classified as merobranchial abanal without interspace. The number of gills on each side is 7.

The central tooth of the radula has rectangular shape with a narrow flexible blade (Figure 12). The first lateral tooth, with a similar appearance to the central tooth, exceeds this one slightly (Figure 12). The major lateral tooth is strongly developed in bicuspid form, with the internal cusp being clearly smaller than the outer cusp (Figure 13).

Holotype: MNCN 15.03/482, 8.5 × 3.8 mm, 1990, "Cangrexo I" expedition. Four valves and the radula were used for SEM, while the rest of the specimen was preserved in alcohol 70%; holotype is the only specimen known.

Type Locality: Off A Quiniela, Galicia, northwestern Spain, 43°17′22″–43°18′52″ N, 09°36′38″–09°35′45″ W, 753–832 m depth ["Cangrexo I" expedition]. It was found between 753–832 m. The type locality is in an area with strong currents, and the holotype was found attached to a rock from a bottom with ferromanganese nodules, calcareous plaques, and coal slag.

Distribution: *Leptochiton* (*L.*) *troncosoi* is a deep-water species, known only from the type locality, off A Quiniela (Galicia, NW Spain).

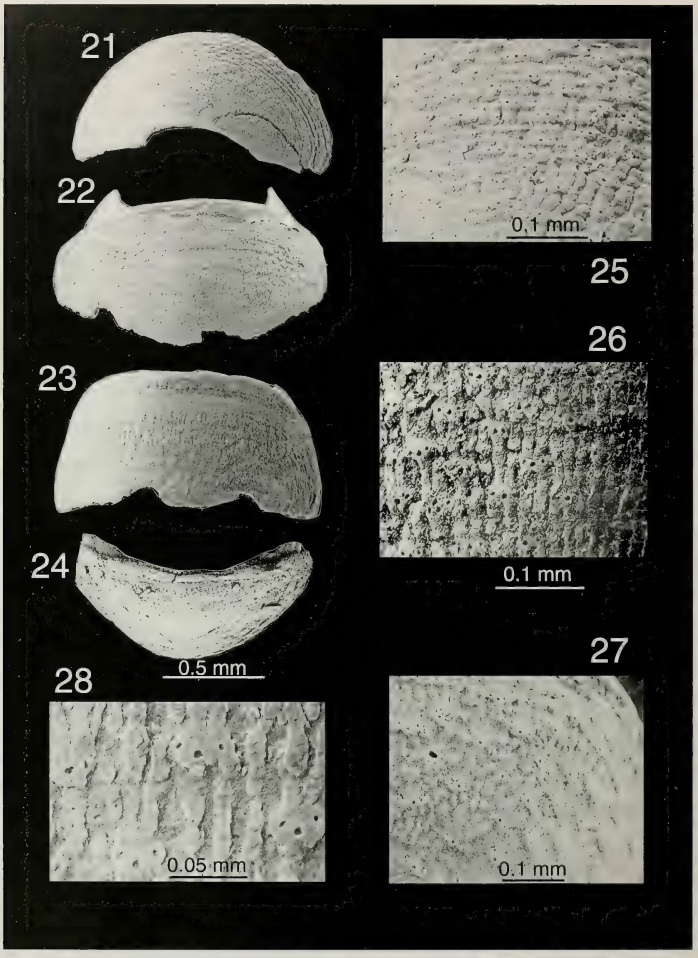
Etymology: The species has been named *Leptochiton* (*Leptochiton*) *troncosoi* in honor of Dr. Jesús S. Troncoso.

Leptochiton (*Leptochiton*) *pepezamorai* new species
(Figures 21–38)

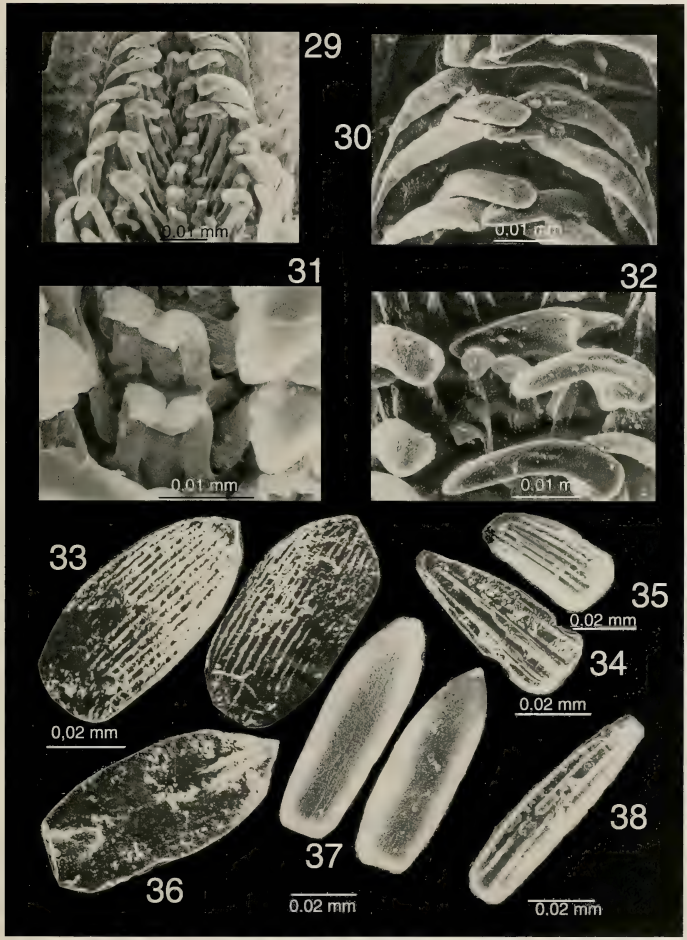
Diagnosis: Characterized by elongate oval shape, dorsal region evenly rounded, not careened, and without a marked apex. The tegmentum is white, although an ochre-oxide coloration is sometimes present. The tegmentum is sculptured with rounded granules. Two or three stems reach along the frontal area to the basal area of the adjacent granule. This creates some furrows on the tegmentum interrupted by the granules and concentric growth lines. The girdle is narrow, covered with rectangular non-overlapping scales. The major lateral tooth of the radula is unicuspid. The spatulate tooth is well developed and it exceeds the major lateral tooth.

Description: The head valve has a semicircular anterior border and the posterior border has a little notch on the apex. The valve presents a strong convex slope (Figure 21). The intermediate valves, clearly rounded in their sides, are dorsally rectangular, except for the second valve, which has a triangular shape. The anterior border of this area is slightly convex, almost straight. The anterior and posterior borders of the remainder of the valves are straight. The lateral areas are not raised, only marked by a change in sculpture (Figures 22, 23). The tail valve is roughly triangular with size similar to the head valve. The mucro is antero-central, prominently marked where the originated slope is slightly convex (Figure 24).

The tegmentum is sculptured with rounded granules and two or three stems on the apical zone, showing a more or less concentric arrangement on the head valve, lateral areas, and postmucral area (Figures 25, 27). On the central areas, the granules are arranged in longitudinal rows separated by shallow grooves. The number of rows varies between 56 and 67.



Figures 21–28. *Leptochiton (L.) pepezamorai.* **21.** Valve I. **22.** Valve II. **23.** Valve IV. **24.** Valve VIII. **25.** Arrangement of pustules on jugal area. **26.** Arrangement of pustules on pleural area. **27.** Arrangement of pustules on lateral area. **28.** Arrangement of megalaesthetes and micraesthetes on pustules.



Figures 29–38. *Leptochiton (L.) pepezamorai.* **29.** Radula. **30.** Spatulate uncinal tooth. **31.** Central and first lateral teeth. **32.** Cusp of major lateral tooth and spatulate uncinal tooth. **33.** Dorsal scale. **34–35.** Dorsal corpuscles. **36.** Ventral scale, dorsal view. **37.** Ventral scales, ventral view. **38.** Marginal spicules.

As a general rule, the stems give striated aspect to the tegmentum, and are interrupted by the granules. In addition, the lateral areas, head valve, and postmucral area always show a variable number of growth marks. Each granule bears three aesthetes. The megalaesthete is located in a central-basal position while the micraesthetes are located in an upper level at both sides.

The articulamentum is white, lacking insertion plates. The apophyses are triangular in shape in the intermediate valves and trapezoid in the tail valve. The wide jugal sinus separates them.

The dorsal girdle is lined with pointed, rectangular, slightly curved scales. They are sculptured with 14 to 16 longitudinal grooves (Figure 33). Their size range is 40–62 μm in length and 25–40 μm on the base. Scattered among these scales are smaller ones, up to 47 μm in length, with 8 longitudinal ribs. Also, the girdle has smooth dorsal spicules up to 160 μm in length. The sharply rectangular ventral scales, up to 65 μm in length, have a weak median, longitudinal rib up to 110 μm in length (Figure 36). The marginal fringe shows pointed conic spicules, which are sculptured with 4 longitudinal ribs (Figure 38). Another, less abundant, type of spicules is present. These have three longitudinal ribs up to 54.4 μm in length.

The gills are located at both sides of the foot, extending from valve VIII to the anus; the gills are classified as merobranchial abanal without interspace.

The central tooth of the radula is rectangular having a well-defined flexible edge. The first lateral tooth, similar in shape to the central tooth, also has a well-defined flexible terminal edge, and exceeds the central tooth slightly in length (Figures 29 and 31). The major lateral tooth is unicuspid with a slightly blunt edge (Figure 29). The spatulate uncinal tooth exceeds the major lateral tooth (Figure 30).

Type Material: Holotype: MNCN 15.03/484, 1.4 × 0.7 mm; Paratype 1, from type locality, Animal Biology Department, Santiago de Compostela University unnumbered, 2.4 × 1.3 mm; Paratypes 2, 3, Animal Biology Department, Santiago de Compostela University unnumbered, 1.75 × 1.2 mm and one broken specimen, "Cangrexo I" Expedition, 43°23′31″ N; 19°32′19″ W, 840 m depth.

Type Locality: 43°17′18″ N, 09°36′35″ W, 753–786 m depth. A strong current was present in the area. The specimens were attached to a rock from a bottom with ferromanganese nodules, calcareous plaques, and coal slag.

Distribution: *Leptochiton* (*L.*) *pepezamorai* is known only from the type locality, A Quiniela (Galicia, NW Spain). It is a deep-water species, found in a depth of 753–840 m.

Etymology: The species has been named *Leptochiton* (*Leptochiton*) *pepezamorai* in honor of Mr. José Zamora.

DISCUSSION

According to the diagnoses given by Kaas and Van Belle (1985) for the genus and subgenus, the species described in this paper are classified in genus *Leptochiton*, subgenus *Leptochiton*.

Both new species differ from the species of *Leptochiton* from the western Atlantic Ocean, South Africa, Pacific, and Indo-Pacific Oceans by the sculptures of their tegmentum, girdle scales, and the number of cusps of their major lateral radular teeth (Kaas and Van Belle, 1985, 1987, 1990, 1994).

Among all the species of *Leptochiton* worldwide, the only one that is considered cosmopolitan is *L. alveolus* (Lovén, 1846) (Kaas and Van Belle, 1985), since it occurs in the Atlantic, Pacific, and Indian Oceans. It differs from *L.* (*L.*) *troncosoi* and *L.* (*L.*) *pepezamorai* by the sculpture of the tegmentum and by the scales of the girdle.

According to the descriptions of Kaas (1979, 1981, 1991), Kaas and Van Belle (1985, 1987, 1990, 1994), Dell'Angelo and Palazzi (1987, 1991), Cesari (1987) and Carmona and Urgorri (1999), *L.* (*L.*) *troncosoi* and *L.* (*L.*) *pepezamorai* differ from the remaining species from the Eastern Atlantic Ocean and Mediterranean Sea by the features below.

In relation to the animal shape, four types have been described: oviform, oblong, oval and elongate oval. *L.* (*L.*) *troncosoi* and *L.* (*L.*) *pepezamorai* are allocated in the fourth type together with *L. alveolus*, *L. cancellatus* (Sowerby II, 1840), *L. cimicoides* (di Monterosato, 1879), *L. scabridus* (Jeffreys, 1880), *L. intermedius* (von Salvini-Plawen, 1968), *L. leloupi* Kaas, 1979, *L. tenuis* Kaas, 1979, *L. sarsi* Kaas, 1981, *L. gascognensis* Kaas and Van Belle 1985, *L. thalattius* Kaas and Van Belle, 1985, *L. geronensis* Kaas and Van Belle, 1985, *L. bedullii* Dell'Angelo and Palazzi, 1986, *L. xanthus* Kaas and Van Belle, 1990, *L. pseudogloriosus* Strack, 1991, and *L. compostellanum* Carmona and Urgorri, 1999.

Of all these species, only *L. tenuis*, *L. thalattius*, *L. geronensis*, *L. xanthus*, and *L. bedullii* have the tegmentum sculptured with granules arranged in longitudinal rows on the central area, and the dorsal scales of the girdle are longer than wide, like in *L. troncosoi* and *L. pepezamorai*.

In relation to the number of cusps of the major lateral teeth of the radula, *L. tenuis* and *L. xanthus* are similar to *L. pepezamorai* and *L. geronensis* is similar to *L. troncosoi*. The radula of *L. thalattius* Kaas and Van Belle (1985) has not been described, but this species differs from *L. pepezamorai* because the tegmentum is not furrowed and the dorsal scales of the girdle are bigger and have a smaller number of ribs.

Leptochiton thalattius differs from *L. troncosoi* by the sculpture of the tegmentum because in the former the central area of the jugal area has about eight parallel rows, is weakly developed, the four or five adjoining rows on the pleurae are curved as result of short interpolated rows (posteriorly as well as anteriorly), the re-

maining pleural rows are parallel, somewhat diverging toward the anterior (Kaas and Van Belle, 1985). The sculpture of *L. troncosoi* has parallel and longitudinal strings on the central area. Besides this, the girdle is dorsally covered with erect scales; among them, calcareous spicules occur and intersegmental spines are found. The scales of *L. troncosoi* are curved and they do not present either dorsal spicules or intersegmental spines.

Comparing *L. pepezamorai* to *L. tenuis*, according to Kaas (1979), the tail valve is much smaller than the other valves, while that of *L. pepezamorai* is of a similar size. The dorsal scales of the girdle of *L. tenuis* are bigger and they have a smaller number of ribs, and the cusp of the major lateral is sharply pointed. In relation to *L. xanthus*, following the description of Kaas and Van Belle (1990), the dorsal scales of the girdle are of smaller size and they have a smaller number of ribs, they lack dorsal spicules and the cusp of the major lateral tooth is sharply pointed.

Taking into account the description of *L. geronensis* by Kaas and Van Belle (1985) it differs from *L. troncosoi* by the tegmentum sculpture of round granules, which are very separated and by having the two cups of the major lateral tooth of similar size.

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Cirsotrema (Gastropoda: Ptenoglossa: Epitoniidae) in the Miocene Chipola Formation of northwestern Florida

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ABSTRACT

The genus *Cirsotrema* is represented in the Lower Miocene Chipola Formation by two species, *Cirsotrema dalli* Rehder, 1945, also present in the Pliocene and Pleistocene of southern Florida and extant in the western Atlantic, and *Cirsotrema cirritum* new species, found only in the Chipola Formation. A search of published records revealed no earlier occurrence of *Cirsotrema dalli* other than its presence in the Chipola Formation.

INTRODUCTION

The family Epitoniidae dates from the Triassic (Clench and Turner, 1950) and by the Cretaceous was well established with worldwide distribution. Sohl (1964: 317) created the genus *Striaticostatum* for seven species from the Cretaceous of the southeastern United States that have features similar to those now placed in *Cirsotrema* Mörch, 1852. The very faint spiral striations on the body whorl of *Striaticostatum* separate it from *Cirsotrema* which has stronger spiral sculpture. Palmer (1937) assigned five species from the Eocene of the southeastern United States to *Cirsotrema* from the Eocene of the same area.

Only two species of *Cirsotrema* have been found in the Lower Miocene Chipola Formation, restricted to that portion of the Chipola Formation in the Chipola River drainage of Calhoun County, Florida, in the region of Tenmile Creek, Farley Creek, and the Chipola River, from State Road 20 north to the mouth of Tenmile Creek. *Cirsotrema dalli* Rehder, 1945, a common species in the Pleistocene Bermont Formation of southern Florida (Hoerle, 1970) and extant in the western Atlantic (Abbott, 1974), is represented in the Chipola Formation by specimens from at least ten separate localities present in the Invertebrate Paleontology collection of the Florida Museum of Natural History at the University of Florida, Gainesville, Florida. Although found throughout the Chipola Formation, *Cirsotrema dalli* is uncommon at any particular locality. A species similar in shell morphology to *Cirsotrema dalli* from the tropical eastern Pacific, *C. togatum* Hertlein and Strong, 1951, ranges from Baja California south to the Galapagos Islands (Keen, 1971). *Cirsotrema togatum* has also been found in the Pliocene Esmeraldas beds of northwestern Ecuador (Pitt, 1981; DuShane, 1988). The new species, *Cirsotrema cirritum*, is also distributed throughout the Chipola Formation within the Chipola River drainage, but has been collected at only five localities and is rare. Three species exhibit a similarity to *Cirsotrema cirritum*. *Cirsotrema acutum* (J. Sowerby, 1813), from the Eocene Barton beds of Great Britain, *Cirsotrema crassicostatum* (Deshayes, 1850), found in the Miocene of Belgium, and *Cirsotrema excelsum* Garcia, 2003, a Recent species from the Indo-Pacific.

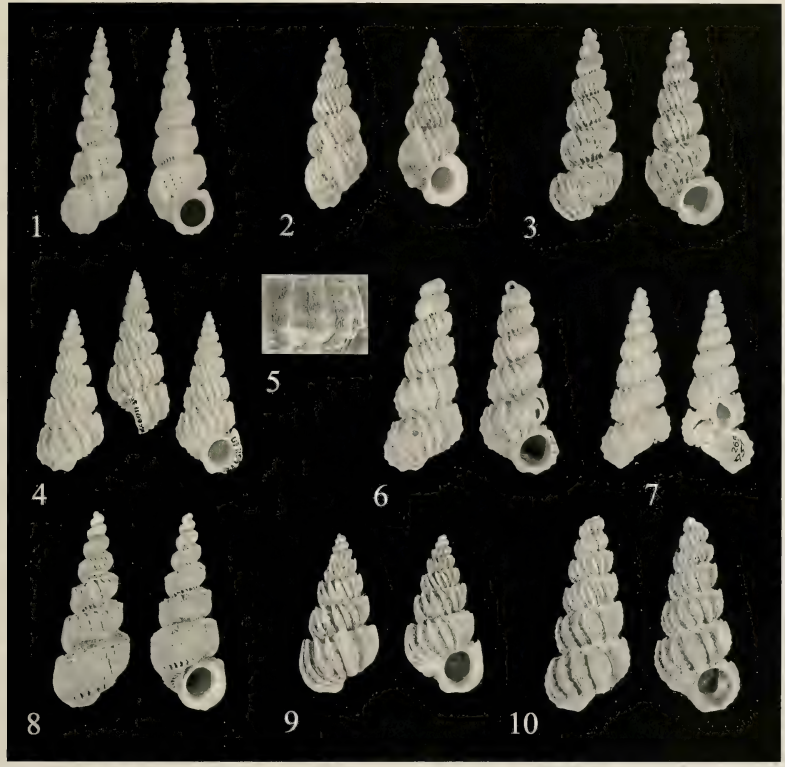
Institutional abbreviations used are: USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; BMNH, British Museum of Natural History, London, England; RMNH, National Museum of Natural History/Naturalis, Leiden, The Netherlands; UF, Florida Museum of Natural History, The University of Florida, Gainesville, Florida, USA; BMSM, The Bailey-Matthews Shell Museum, Sanibel, Florida, USA; LACM, Los Angeles County Museum of Natural History, Los Angeles, California, USA. "P. Diegel collection" refers to the collection of Phyllis Diegel, West Palm Beach, Florida, USA. "Sunderland collection" refers to the collection of Kevan and Linda Sunderland, Sunrise, Florida.

SYSTEMATICS

Superfamily Janthinoidea Lamarck, 1812
Family Epitoniidae Berry, 1910
Genus *Cirsotrema* Mörch, 1852
Cirsotrema Mörch, 1852: 49.

Type Species: *Scalaria varicosa* Lamarck, 1822, by monotypy.

Diagnosis: Shell white to gray, turriculate; body whorl usually with broad spiral cords, often covered with fine spiral and axial lines forming microscopic reticulate sculpture. Raised axial lines forming microscopic reticulate sculpture. Raised axial costae composed of numerous lamellations, frequently foliated, sometimes covering entire body whorl, with or without prominent varices. All possess a basal ridge. Aperture circular to oval.



Figures 1–10. *Cirsotrema* species. **1.** *Cirsotrema dalli* Rehder, 1945, Recent, Anses d'Arlets, Martinique, height 43.8 mm, width 13.5 mm, P. Diegel collection. **2.** *Cirsotrema pilsbryi* McGinty, 1940, Recent, taken off St. Augustine, Florida, by Ted Yocius, height 15.3 mm, width 6.4 mm, Sunderland collection. **3.** *Cirsotrema dalli* Rehder, 1945, fossil, UF 45354, Chipola Formation, Tenmile Creek, Calhoun County, Florida, height 18.3 mm, width 7.0 mm. **4–7.** *Cirsotrema cirritum*, new species. **4.** Holotype, UF 110972, height 30.1 mm, width 11.8 mm. **5.** Paratype, UF 112019, sculpture of teleoconch, scale bar = 5 mm. **6.** Paratype, BMSM 15301, height 54.1 mm, width 22.0 mm. **7.** Paratype, USNM 522028, height 50.4 mm, width 18.2 mm. **8.** *Cirsotrema* cf. *woodringi* Olsson, 1967 (= "*C. arcella* Rehder", Woodring, 1959), UF 112142, Gatun Formation, road cut east of Cativa, Province of Colón, Panama, height 36.0 mm, width 13.6 mm. **9.** *Cirsotrema acutum* (J. Sowerby, 1813), UF 112018, Barton Clay Formation, Barton on Sea, Hampshire, England, height 16.2 mm, width 7.7 mm. **10.** *Cirsotrema crassicostatum* (Deshayes, 1850), RMNH Lot 497 (No. 65166?), Zanden V. Antwerpen, height 37.3 mm, width 14.9 mm.

Cirsotrema dalli Rehder, 1945
(Figures 1, 3)

Cirsotrema (Cirsotremopsis) dalli Rehder, 1945: 128; Olsson, 1967: 40, pl. 5, figs. 2–2b.

Cirsotrema (Cirsotremopsis) arcella Rehder, 1945: 128; Olsson, 1967: 40, pl. 5, figs. 4–4a.

Cirsotrema arcella Rehder, Clench and Turner, 1950: 228, pl. 98, fig.3, [considered by Clench and Turner to be conspecific with *C. dalli*].

Cirsotrema dalli Rehder, Clench and Turner, 1950: 227–228, pl. 98, fig. 1, 3; Warmke and Abbott, 1961: 71–78, pl. 14, fig. H; Morris, 973: 154, pl. 44, fig. 1; Abbott, 1974: 114, fig. 1188; Humfrey, 1975: 91, pl. 7, fig. 12; Rios, 1975: 57, pl. 15, fig. 219; Abbott and Dance, 1982: 69; Sunderland, 1990: 14; Rios, 1994: 99, pl. 33, fig. 404.

Description: Shell medium to large, turriculate; teleoconch whorls 9 or 10, convex, with 5 or 6 broad spiral cords overlain with fine spiral and axial lines, forming a microscopic reticulated sculpture. Suture deep. Fimbrious axial costae composed of fine, wavy lamellae, with a crosshatched pattern inclined upwards abaperturally, hooked at shoulder, sinuous, with alternating waves so that each succeeding costa contacts abapertural costa, forming a secondary surface which is almost flat or slightly convex, leaving only very small holes or pits. Prominent varices present at irregular intervals. Aperture subcircular; with labral varix.

Holotype: USNM 515240

Type Locality: 29°14′ N, 85°29′ W, off Cape San Blas, Florida, in 25 fathoms.

Remarks: Some authors consider *Cirsotrema dalli* to be a junior synonym of the Recent *Cirsotrema cochlea* (G. B. Sowerby II, 1844) from the eastern Atlantic (Clench and Turner, 1950: 228; Weil, et al., 1999: 14). Also, *Cirsotrema cochlea* may be a junior synonym of *Cirsotrema pumicea* (Brocchi, 1814). A comparative study of the relationship between *C. dalli, C. cochlea,* and *C. pumicea* has not been made and is beyond the scope of this paper.

Cirsotrema togatum may be considered the eastern Pacific cognate of *C. dalli.* Both have fimbriated costae frequently covering the entire surface, similar overall shapes, and varices at irregular intervals. Both may also have costae of varying widths due to erosion, especially on fossil specimens. The costae of dead collected Recent specimens are frequently eroded, as are the early whorls of live-taken specimens, exposing the sculpture on portions of the body whorl. A figure of a Recent specimen of *Cirsotrema togatum* by Keen (1971, fig. 633) and figures of Pliocene specimens by Pitt (1981, figs. 2, 3) and DuShane (1988, figs. 10, 11, 12) show specimens morphologically similar to *C. dalli.*

DuShane (1974, figs. 54 and 55) illustrated two specimens of *Cirsotrema togatum.* DuShane's figure 54, a live-taken specimen, is similar to the Recent specimens examined by this author, with the costae extending up over the suture and onto the preceding whorl, the suture subdued by the surface sculpture, and lacking a noticeable shoulder on the whorls, giving a somewhat straight appearance to the whorl profile. DuShane's figure 55, the holotype, exhibits a definite indentation at the suture with shouldered costae and some exposed intercostal areas, very similar to the holotype of *Cirsotrema dalli.* The discrepancy between DuShane's figure 54 and the holotype of *Cirsotrema togatum* illustrated in figure 55 might be resolved by the description of the Recent specimen illustrated in figure 54 as a separate, new species.

Although somewhat similar to *Cirsotrema dalli, C. pilsbryi* McGinty, 1940, a Recent species endemic to the western Atlantic, is easily distinguished from this species. The wavy costae of *Cirsotrema dalli* touch each other to a varying extent, forming a secondary superficial surface and leaving only small holes or pits between the adherent portions of the costae, obscuring the surface of the whorl itself, while the costae of *C. pilsbryi* are more sloping at the shoulder, with a subdued hook, giving the surface of the costae a more rounded appearance than that of *C. dalli.* Also, the costae of *Cirsotrema pilsbryi* consist of wavy lamellations without the foliations or crosshatched effect of the costae of *C. dalli.* Both *Cirsotrema dalli* and *C. pilsbryi* have irregularly spaced varices, have a microscopic reticulated sculpture on the body whorl, and have broad spiral cords which angle slightly towards the apex adaperturally, rather than revolving parallel to the whorl, although the sculpture on the body whorl is frequently not visible under the secondary surface on *C. dalli.* The principal characteristics separating *Cirsotrema dalli* from *C. pilsbryi* are well illustrated in Sunderland (1989, 1990).

The Recent Indo-Pacific *Cirsotrema ernestoilaoi* Garcia, 2001, is easily separated from *C. dalli* by the trapezoidal shaped (with wide shoulder) profile of the whorl formed by the axial costae, and lack of pits or holes in the surface sculpture of *C. ernestoilaoi.*

Cirsotrema woodringi Olsson, 1967, a rare species currently found only in the Miocene Gatun Formation of Panama and the Pliocene Tamiami Formation at Sunnyland, Florida, has foliated costae similar to *C. dalli.* It differs by the straight line separating the costae, which abut, completely covering the surface of the whorl. *Cirsotrema dalli* has wavy costae leaving small pits or openings in the secondary surface formed by the costae. As Olsson so aptly stated in reference to *Cirsotrema woodringi* (also applicable to *C. dalli* regarding costae), "General surface has a finely porous texture resembling that produced by a linen cloth" (1967: 41). This feature may be attributed to intritacalx (D'Attilio and Radwin, 1971), a shell layer not well studied in the Family Epitoniidae.

Olsson (1967: 41) reported a specimen of *Cirsotrema dalli* from "McClellan Farm", a locality on the west bank of the Chipola River south of Tenmile Creek, which he stated "was carefully compared with the type of *C. dalli,* a Recent species, and no distinguishing difference could be found".

Cirsotrema cirritum new species
(Figures 4–7)

Description: Shell medium to large, turriculate. Early whorls missing on all specimens examined. First existing whorl of holotype (last protoconch whorl) with sculpture ranging from smooth to ¼ turn with several single microscopic wavy axial lamellae that gradually enlarge into foliated costae. No clear distinction between protoconch

and teleoconch present. Teleoconch with 8 tumid whorls. Suture deep. Axial costae 13 on last whorl, strongly recurved, hooked, and angled slightly adapertur-ally on shoulder, extending in a straight line over suture; surface of costae composed of multiple wavy lamella with very fine irregular diamond or square pattern; pattern inclined abapertur-ally. Intercostal spaces variable, usually wider than costae, with 5 broad, rounded spiral cords, overlain with 8 to 12 much finer cords, crossed by equally fine axial growth lines so as to form a microscopic, reticulated pattern. Reticulated pattern continue from intercostal spaces to cover adapertural side of recurved costae. Top of wavy axial costae sharp. Broad spiral cords on intercostal spaces reproduced on abapertural surface of costae and angled 45° apically. Adaptertural surface of costae covered with wavy cross-hatched lamellae. Fine line of demarcation separates leading edge of costae where joined by succeeding intercostal space. Anterior reflected projections on axial ribs of last whorl forming coarse, undulating basal ridge. Varices absent. Aperture holostomatous.

Holotype: UF 110972, height 30.1 mm, width 11.8 mm.

Paratypes: BMSM 15301, protoconch missing, height 54.1 mm, width 22.0 mm, 30°28.030′ N, 85°09.572′ W (= Tulane University locality TU 458), east bank of Chipola River, above Farley Creek, (SW ¼ Sec. 10, T1N, R9W), Calhoun County, Florida, Chipola Formation; USNM 522028, spire and aperture missing, height 50.4 mm, width 18.2 mm, 30°29.44′ N, 85°11.17′ W, (= Tulane University locality TU 951, = United States Geological Survey locality 26578), Tenmile Creek, about 2 km west of Chipola River, (SE ½ Sec. 12, T1N, R10W), Calhoun County, Florida, Chipola Formation; UF 67746, spire missing, height 29.8 mm, width 10.3 mm, 30°27.45′ N, 85°08.45′ W, (= Tulane University locality TU 825), Farley Creek at abandoned mill about 350 m west of bridge on Florida Highway 275 (SW ¼ Sec. 21, T1N, R9W), Calhoun County, Florida, Chipola Formation; UF 112019, body whorl only, with aperture, height 16.5 mm, width 20.1 mm, same locality as previous specimen.

Type Locality: 29°30.05′ N, 85°11.00′ W, Tenmile Creek, at power line crossing about 1.6 km west of Chipola River (SE ¼ Sec. 7, T1N, R10W), Calhoun County, Florida, Chipola Formation.

Etymology: The name *cirritum* is derived from the Latin *cirrus* meaning "filamentous", referring to the fringed costae of the new species.

Discussion: All specimens of *Cirsotrema cirritum* examined lack the apical whorls. It may be assumed that the missing whorls consist of 1 to 3 smooth whorls as evidenced by the remainder of a partial smooth protoconch whorl on the holotype. The width of the axial costae and the intercostal spaces appear to be a variable characteristic on all specimens studied. Features which the eastern Pacific *Cirsotrema togatum* and the western Atlantic *C. dalli* have in common with *C. cirritum* are turreted shape, sculpture on the surface of the costae, and spiral cords with microscopic reticulated sculpture on the body whorl. *Cirsotrema cirritum* differs from *C. togatum* and *C. dalli* by its larger size, narrower costae, wider intercostal areas, and lack of varices. Although the foliated face on the costae of *Cirsotrema togatum* and *C. dalli* presents a flat surface, the foliated adapertural surface of the costae of *C. cirritum* is recurved. Also, a sharply impressed line of demarcation separates each costa from the succeeding intercostal space and next costa on *C. cirritum*, indicating a pause in growth.

The *Cirsotrema* species from the Eocene of the southeastern United States are all under 30 mm, have narrower spiral cords, and lack the reticulated sculpture on the intercostal areas and the crosshatched effect present on the costae of *C. cirritum*. The Eocene *Cirsotrema acutum* (J. Sowerby, 1813) from Great Britain, and the Miocene *C. crassicostatum* (Deshayes, 1850) from Europe are very similar to each other. Both have longitudinal laminations on the costae without the cross-hatched effect of *Cirsotrema cirritum*, have narrower, more pronounced spiral cords, and lack the axial striations present on the intercostal spaces of *C. cirritum*. *Cirsotrema acutum* is also smaller and more attenuate posteriorly than *C. cirritum*.

There is no identifiable sculpture visible on Maury's (1925: 242, pl. 37, fig. 4) figure of a very eroded single whorl of the holotype of *Cirsotrema tamanensis* (Maury, 1925) from the Miocene of Trinidad.

Several Recent Indo-Pacific species of *Cirsotrema* have features similar to *C. cirritum*. *Cirsotrema plexis* Dall, 1925, and *C. fimbriatulum* (Masahito, Kuroda and Habe, 1971) may be distinguished from *C. cirritum* as both have varices and have about 20 axial costae on the body whorl as opposed to 13 on *C. cirritum*. Varices are lacking on *Cirsotrema rugosum* (Kuroda and Ito, 1961) and *C. excelsum* Garcia, 2003, but both have a greater number of axial costae on each whorl and the costae differ in sculpture from those of *C. cirritum*. The sculpture on the surface of the axial costae of *Cirsotrema richeri* Garcia, 2003, most closely resembles that of the costae of *C. cirritum*. A greater number of axial costae on the body whorl and the presence of varices on *Cirsotrema richeri* separates it from *C. cirritum*.

Cirsotrema cirritum has only been recorded from the Chipola Formation of northwestern Florida. *Cirsotrema dalli*, which may have originated in the Lower Miocene Chipola Formation, extended its range over southern Florida during the Pliocene and Pleistocene epochs, and survives in the Recent of the western Atlantic Ocean.

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A new species of *Stramonita* (Gastropoda: Muricidae) from the Late Pliocene of Florida

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ABSTRACT

Stramonita penelaevis new species from the Caloosahatchee Formation of southeastern Florida is a smooth rocky-shore muricid gastropod. *Stramonita penelaevis*, the first member of its clade from Florida, represents a group that has become geographically restricted to the South Atlantic since the late Pliocene.

INTRODUCTION

Muricids of the subfamily Rapaninae are common members of rocky-shore faunas throughout the tropics, but they are uncommon as fossils. The known fossils document surprising patterns of geographic restriction during Neogene times (Vermeij, 2001). In tropical America, for example, the genus *Neorapana* Cooke, 1918, is known today only as three eastern Pacific species, but during the early Miocene the genus was also present on the Caribbean coast of Venezuela (Gibson-Smith et al., 1997). A group of species today represented by the South Atlantic *S. bicarinata* (Blainville, 1832) occurred in the Caribbean during the late Miocene (Vermeij, 2001).

The genus *Thaisella* Clench, 1947, found in the western Atlantic today from Central America and the southern Caribbean to Brazil, was represented in the late Pliocene Caloosahatchee Formation of Florida by a species that has since contracted its range to the southern Caribbean (Petuch, 2004). The eastern Atlantic and Mediterranean species *Stramonita haemastoma* (Linnaeus, 1767) made a brief western Atlantic appearance in the early Pleistocene Bermont Formation of Florida, temporarily coexisting with native western Atlantic members of the *Stramonita haemastoma* group that have existed there from early Miocene to Recent times (Vermeij, 2001).

In this paper we describe a new species of the rapanine muricid genus *Stramonita* Schumacher, 1817, *S. penelaevis*. This species is the first member of its group (the *S. bicarinata* group) known from Florida, and strengthens the case for post-Pliocene geographic restriction of its clade. Despite the worn condition of the material, the distinctiveness and geographic peculiarities of the new species prompt us to name and describe the material.

SYSTEMATIC PALEONTOLOGY

Genus *Stramonita* Schumacher, 1817
Stramonita penelaevis new species
(Figures 1–5)

Type Species: *Stramonita haemastoma* (Linnaeus, 1767).

Diagnosis: Ovate-elongate *Stramonita* with five denticles inside outer lip, obsolete axial waves on last whorl, and very low undifferentiated spiral cords.

Description: Shell small for genus, maximum length 40.5 mm, not constricted abapically; all specimens heavily worn; teleoconch consisting of four preserved whorls separated by indistinct, appressed sutures; axial sculpture of last whorl consisting of about seven very low, very broad, barely perceptible swellings or waves; traces of spiral cords present, revealing low, undifferentiated cords, which do not form nodes; aperture elongate-ovate; outer lip abraded at edge, thickened, its inner side bearing five prominent denticles; a second row of denticles situated further inside aperture; inner lip smooth, its abapertural margin slightly recessed; adapical end of inner lip with prominent parietal tooth; siphonal fasciole low, broad, rounded; umbilical slit absent.

Type Locality: Caloosahatchee Formation, Palm Beach Aggregates (GKK Rock Pit), off State Road 80, Loxahatchee, Palm Beach County, Florida.

Holotype: UF 114426, shell length 36.5 mm, diameter 24.4 mm.

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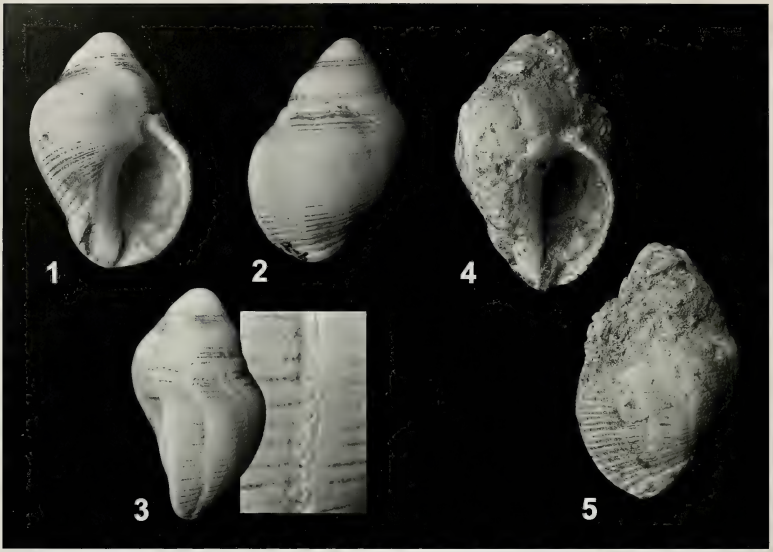

Figures 1–5. *Stramonita penelaevis* new species. **1–3.** Holotype, UF 114426, shell length 36.5 mm, shell diameter 24.4 mm. **1.** Ventral view. **2.** Dorsal view. **3.** Lateral view of the outer lip showing two growth checks in close succession and the terminal lip. Enlarged image of first growth check behind terminal lip shows well-preserved sharp crenulated (toothy) edge, which has been worn away on terminal lip. **4–5.** Paratype A, UF 114427, shell length 40.5 mm, shell diameter 25.3 mm. **4.** Ventral view. **5.** Dorsal view.

Paratype: UF 114427, shell length 40.5 mm, shell diameter 5.3 mm.

Etymology: Latin *pene,* almost; and *laevis,* smooth.

Remarks: *Stramonita penelaevis* is most similar to the Recent *S. bicarinata* (Blainville, 1832) from the South Atlantic islands of St. Helena and Ascension. The new species differs from *S. bicarinata* in having obsolete axial sculpture and lacking the two rows of nodes characteristic of *S. bicarinata.*

The new species also resembles *S. quadridentata* (Vokes, 1989) from the late Miocene of the Dominican Republic and Panama (see also Vermeij, 2001). The latter species is even more sculptured than *S. bicarinata,* and like that species has four to five denticles on the inner side of the outer lip.

Together with the early Miocene *S. semiplicata* Vermeij, 2001, from the Cantaure Formation of Venezuela, these three species—*S. bicarinata, S. penelaevis,* and *S. quadridentata*—form a group (and probable clade) of species in *Stramonita* with distinct denticles instead of continuous lirae on the inner side of the outer lip. As pointed out by Vokes (1989), similar species occur in the Neogene of Europe.

Vermeij (2001) suggested that the South Atlantic *S. bicarinata* is part of a clade that during late Neogene times was more widespread in tropical America. He noted that the eastern Pacific genus *Acanthais* Vermeij and Kool, 1994 (represented by the single Recent species *A. brevidentata* (Wood, 1828)), is related to the Atlantic *S. bicarinata* group. *Acanthais* differs from these species of *Stramonita* by possessing a labral tooth and by having a prominent, central columellar fold. The latter feature is present but reduced in *S. semiplicata* from the early Miocene of Venezuela. The discovery of *S. penelaevis* in the Caloosahatchee Formation (late Pliocene) of Florida provides further evidence that the *S. bicarinata* group was more widely distributed in the Atlantic during Miocene and Pliocene times than it is today. The new species represents the first and only record of this group of species in the Caloosahatchian biogeographic province of Petuch (1982).

ECOLOGY

The new species of *Stramonita* described here is unusual among members of *Stramonita* in being almost smooth. The near absence of axial sculpture in *S. penelaevis* could be the result of abrasion, but the denticulate sculpture on the inner side of the outer lip is well preserved. We are therefore inclined to the view that the strongly reduced external sculpture is real. In the Recent fauna, such major sculptural reduction characterized species that occupy surf-swept rocky shores. Examples include *Purpura persica* (Linnaeus, 1758) from the western Pacific; *Thais meretricula* Röding, 1798, at the islands of Fernando de Noronha (off Brazil) and Ascension; and some populations of *Acanthais brevidentata* in the eastern Pacific. These observations lead us to surmise that the new species of *Stramonita* lived in a heavily waveswept environment. Habitats like this yield few fossils. Co-occurring with *S. penelaevis* at the type locality of *S. penelaevis* in the Caloosahatchee Formation are specimens of an almost smooth-shell population that we tentatively assign to the *S. haemastoma* (Linnaeus, 1767) complex. Specimens of this population as well as those of *S. penelaevis* are worn, indicating probable transport by currents from a wave-swept shore to depths where sedimentation takes place.

ACKNOWLEDGMENTS

We thank Edward Petuch for taking Herbert to the locality from which our new species comes, and Janice Cooper for technical assistance.

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A new *Orbitestella* (Gastropoda: Heterobranchia: Orbitestellidae) from Tierra del Fuego, Argentina

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ABSTRACT

A new species of *Orbitestella* is described from Tierra del Fuego, Argentina. The morphology of the jaws is the main character used for the generic allocation. *Orbitestella patagonica* new species is characterized by a widely umbilicated shell with low spire, ornamented with numerous, regularly distributed, spiral threads and weak sinuous commarginal growth lines. The entire surface of the protoconch is covered with crisp spiral threads. Examination of the anatomy revealed the presence of a relatively small stomach and the posterior region of genital system bulging into haemocoel space as main distinguishing characters.

INTRODUCTION

The Orbitestellidae are extremely minute, discoid, and widely umbilicated gastropods, living mainly in the Southern Hemisphere (Ponder, 1967, 1990; Powell, 1979). The genus *Orbitestella* Iredale, 1917 has a virtually worldwide distribution, although most of the known species occur in Australia and New Zealand (Ponder, 1990; Ponder and Keyzer, 1998). In the north Atlantic, two species have been described by Rolán and Rubio (1992): *O. similis* from Cape Verde and *O. cubana* from Cuba. The only species of the genus presently known from off South America is *Orbitestella ponderi* Linse, 2002, a species described from the East Beagle Channel (Tierra del Fuego). Linse (2002) identified as *O. ponderi* specimens from southern Chile previously reported by Ponder (1990) as *Orbitestella* sp.

Orbitestella has previously been placed in the Trochoidea or Truncatelloidea, either in the Omalogyridae or Orbitestellidae (Iredale, 1917; Thiele, 1929; Knight et al., 1960). Ponder (1967), based on the structure of the animals and radula, placed *Orbitestella* in the Rissooidea [as Rissoacea]. This point of view was followed by several subsequent authors (Powell, 1979; Ponder, 1983; Marshall, 1988; Hickman and McLean, 1990). Later on, Ponder (1990) after having studied the anatomy of two orbitestellid species [*Orbitestella wareni* Ponder, 1990, and *Microdiscula charopa* (Tate, 1899)] suggested that Orbitestellidae should not be considered as rissooidean but as primitive Heterobranchia, related to the northern-hemisphere freshwater family Valvatidae. Ponder and Warén (1988) placed Orbitestellidae in the Valvatoidea.

In the present paper a new species of *Orbitestella* from the Magellanic Region is described on the basis of shell morphology and general anatomy.

MATERIALS AND METHODS

The studied specimens were collected at the Beagle Channel, Tierra del Fuego, Argentina (Figure 1). Samples were taken with a dragnet, fixed in 10% buffered formalin and transported to the laboratory where mollusks were sorted from sediments using a stereoscopic microscope, and preserved in 70% ethanol. Shell, radula, jaws, and operculum morphology were studied and illustrated using scanning electron microscopy (SEM). For anatomical studies specimens were decalcified in Railliet-Henry's solution. Two specimens were processed for histology. Semi-thin sections (0.3 μm thick) were stained with Mallory's trichrome (Gabe, 1968). Additionally, 5 specimens were dissected under stereomicroscope. It was not possible to study the right side of these specimens (i.e. pallial tentacle, penis, and propodial flap).

Voucher specimens were deposited in the Museo de La Plata (MLP) and Museu de Zoologia da Universidade de São Paulo (MZSP).

Abbreviations used in the figures: **ad**, anterior lobe of digestive gland; **an**, anus; **ca**, capsule gland; **ce**, cerebral ganglion; **cg**, pallial genital gland; **cm**, columellar muscle; **cs**, crystalline style sac; **dg**, digestive gland; **es**, esophagus; **ey**, eye; **fs**, foot sole; **ft**, foot; **h**, heart; **go**, hermaphrodite gonad; **gp**, pedal ganglion; **hy**, inner shell organic layer (hypostracum); **in**, intestine; **jw**, jaw plate; **mb**, mantle border; **mf**, mantle U-shaped fold; **mg**, mantle gland; **mo**, mouth; **od**, odontophore; **ol**,

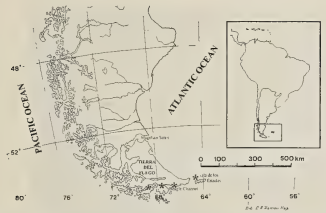


Figure 1. Map showing the type locality (⊗) of *Orbitestella patagonica* new species and new findings of *O. ponderi* (*).

periostracum; **op**, operculum; **os**, osphradium; **pa**, posterior lobe of pedal gland; **pe**, periostracum; **pg**, posterior mucous gland; **po**, pigmented mantle organ; **pr**, propodium; **pt**, prostate; **ro**, renal organ; **sg**, salivary gland; **st**, stomach; **sv**, seminal vesicle; **sy**, statocyst; **te**, cephalic tentacle.

SYSTEMATICS

Genus *Orbitestella* Iredale, 1917 (Type species: *Cyclostrema bastowi* Gatliff, 1906, by original designation)

Orbitestella patagonica new species
(Figures 2–18)

Diagnosis: Shell minute, discoid, with low spire, widely umbilicated, ornamented with weak sinuous commarginal growth lines and numerous, regularly distributed spiral threads. Protoconch with crisp spiral threads covering entire surface. Radula with wide, pectinated rachidian tooth with sharply pointed cusps; lateral tooth plate-like, with a main cusp and sparsely serrated outer margin; marginal tooth slender, sickle-like. Stomach relatively small.

Description: Shell (Figures 2–6, 8–10): Minute (maximum diameter 1.1 mm), discoid, widely umbilicated, thin, translucent, shiny, up to 2.75 rounded and regularly expanding whorls; spire depressed, slightly raised (Figures 2–5). Color yellowish-buff. Periostracum thin, colorless. Protoconch formed by 0.75 whorl, about 200 μm wide; initially only sculptured with low granulations, followed by 10–12 spiral threads (Figure 6). First 0.25 whorl weakly marked by straight growth disruption (Figure 6). Teleoconch of up to 2 rounded whorls, suture incised. Umbilicus deep, wide, representing about 32 % of maximum shell diameter (Figure 5). Shell surface with weak, sinuous commarginal growth lines and numerous, regularly distributed and fine spiral threads (Figure 8), also visible inside umbilicus (Figure 5); first whorl of teleoconch with about 10 spiral threads, last whorl with 35–37. Shell aperture nearly circular (about 240 μm high by 270 μm wide) with sinuous peristome (Figures 4, 5).

Shell ultrastructure: Only one well-defined crossed-lamellar layer, about 25 μm thick (Figure 9). Organic layer (hy), a third of periostracum thickness, made more evident in decalcified shell (Figure 16).

Head-foot (Figures 11, 16): Color cream-yellowish, uniform in preserved specimens. Head inlaid into foot (Figure 11). Pair of cephalic tentacles well developed. Eyes relatively large, sunken into integument medially between bases of cephalic tentacles; lens solid, volume about half that of eyes (Figure 16). A pair of tentacle-like flaps (sometimes referred to as a "snout") lying between tentacle bases, flanking mouth. Foot somewhat massive, cylindrical when retracted, occupying ¼ whorl; sole entirely covered by long cilia. Columellar muscle thick. Posterior mucous gland occupying posterior and middle region of foot.

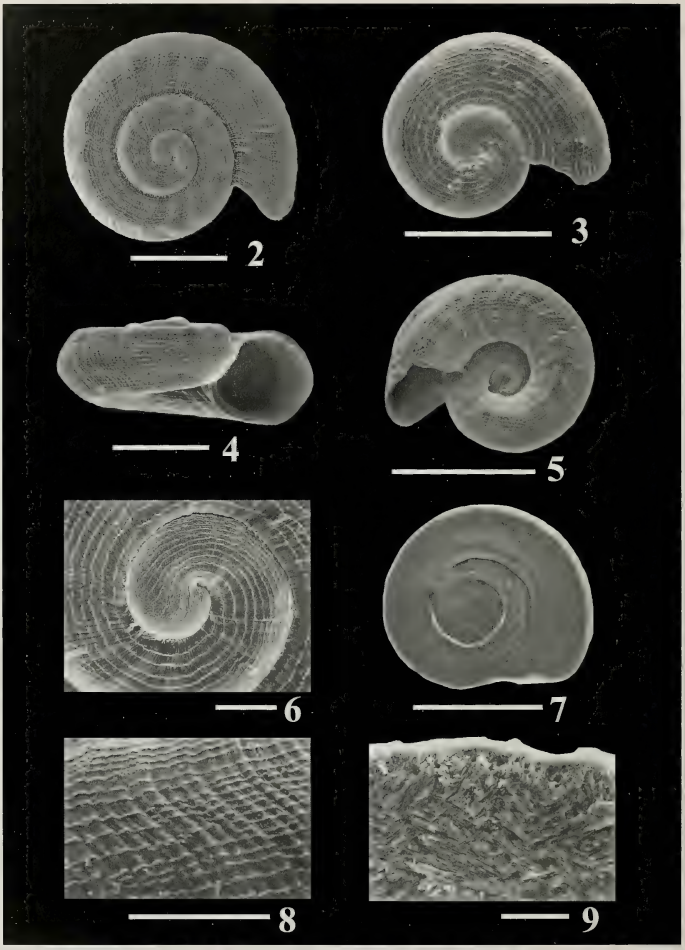
Operculum (Figure 7): Nearly circular, paucispiral, up to 3.5 slightly overlapping whorls, horny, thin, translucent, yellowish; nucleus subcentral.

Pallial Cavity (Figures 16, 17): Expanded by ¼ whorl, with thin, simple mantle border. Gill absent. U-shaped low fold, sometimes described as "a short, partially ciliated lobe", dorsally located (Figure 17, mf). Osphradium small, fold-like, ciliated, located on left side. Pigmented mantle gland (seen by transparency) circular, thin, relatively small, color dark brown, surface uniform, located at middle-posterior part of roof of pallial cavity (Figure 9, po).

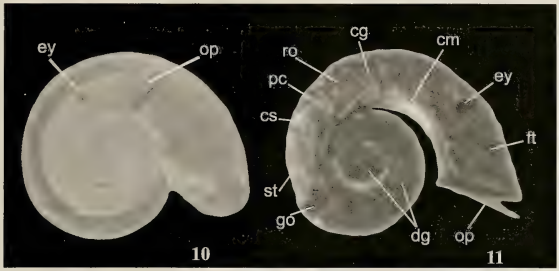
Visceral mass (Figures 11, 16, 17): Comprising two whorls. Digestive gland almost fully developed on last whorl. Stomach and gonad located in first half of visceral whorls, stomach in right side, gonad in left (Figure 16).

Circulatory and excretory systems (Figure 16): Heart small, located between stomach and renal organ, posterior to pallial cavity. Renal organ triangular in section.

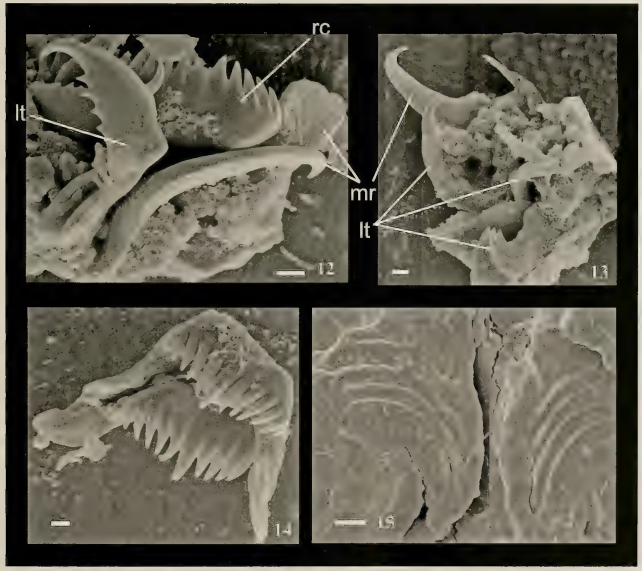
Digestive system: **Mouth** on a small protuberance, between tentacle-like flaps (Figure 16). Oral tube narrow, laterally expanded. **Jaw plates** large, rounded, laterally located and flanked by well-developed muscles (Figure 16); with five serrated rows of simple curved plates, posteriorly concave, on each side of inner surface (Figure 15). Odontophore similar to jaws in size, with several small muscles, but no cartilages (Figure 16). **Radula** 1:1:1:1:1, somewhat longer than odontophore. (Figure 12). **Rachidian tooth** large, trapezoidal, with peg-like lateral edges and an excavated base; cutting edge pectinated, wide, strongly curved inwards, bearing 11−13 slender and sharply pointed cusps, gradually becoming smaller in outward direction; central cusp straight; lateral cusps somewhat curved, narrower than central one (Figure 14). **Lateral teeth** plate-like with straight base; cutting edge with a large primary cusp, 4–5 smaller and regularly separated cusps on outer side, and a small inner side cusp, on base of primary cusp (Figure 12). **Marginal teeth** sickle-like, slender, gradually narrowing to sharply pointed tip; secondary cusps,



Figures 2–9. *Orbitestella patagonica* new species. **2.** Holotype, MLP 6367. **3–7.** Paratypes, MLP 6368. **3.** Dorsal view. **4.** Lateral view. **5.** Ventral view. **6.** Detail of the protoconch. **7.** Operculum. **8.** Shell surface sculpture. **9.** Shell ultrastructure. Scale bars: Figures 2–4 = 300 μm; Figures 5 = 500 μm; Figures 6–8 = 100 μm; Figure 9 = 20 μm.



Figures 10–11. *Orbitestella patagonica.* Paratypes, MZSP 38708. **10.** Dorsal view of a specimen seen by transparency. **11.** Right view of a specimen removed from shell. Scale bars = 600 μm.



Figures 12–15. *Orbitestella patagonica.* SEM micrographs of the radula (MZSP 38708). **12.** Rachidian (**rc**), lateral (**lt**) and marginal (**mr**) teeth (dislodged). **13.** Detail of lateral (**lt**) and marginal (**mr**) teeth. **14.** Detail of rachidian teeth. **15.** Jaws. Scale bars = 1 μm.

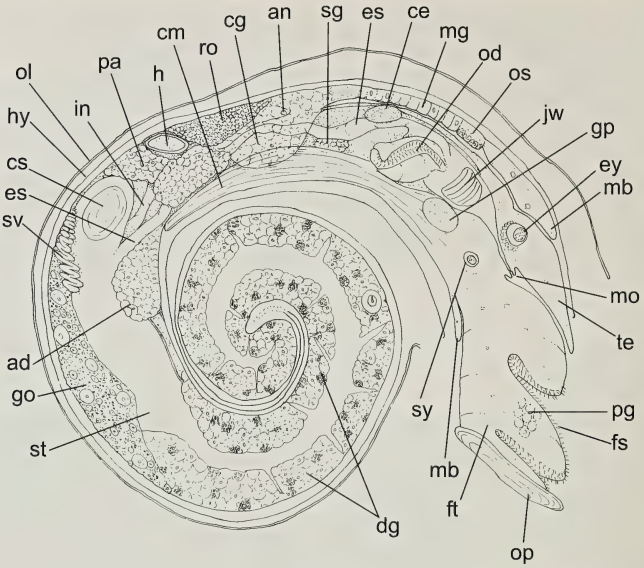
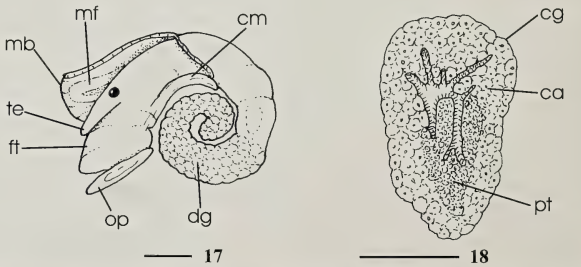


Figure 16. *Orbitestella patagonica.* Semi-diagrammatic longitudinal section. Scale bars = 100 μm. Abbreviations in Materials and Methods.



Figures 17–18. *Orbitestella patagonica.* Anatomical details. **17.** Left side view of a specimen with pallial cavity sectioned and deflected; **18.** Transversal section in middle region of common glandular genital duct. Scale bars: Figure 17 = 100 μm; Figure 18 = 50 μm.

absent (Figures 12, 13). Esophagus originating from middle dorsal region of odontophore, initially narrow, wider posteriorly, entering stomach at anterior-ventral region at side of style sac (Figure 16); esophagus wall thick and undulated by presence of glands. Salivary glands small, ventral to esophagus and posterior to odontophore. Stomach large occupying about ¼ whorl, somewhat flat, on right side of visceral mass (Figures 10, 16). Inner gastric surface covered by cuticle. Style sac small, located in antero-dorsal region of stomach, bearing an ovoid crystalline style. Stomach lumen continuous with digestive gland. Digestive gland composed by non-pigmented vacuolar cells. Intestine short (a half of esophagus length), originating between stomach and style sac, directed forward (Figure 16). Anus located on posterior end of pallial cavity.

Genital system: Gonad hermaphrodite, located between stomach and digestive gland, at left side posterior to pallial cavity, occupying 0.5 whorl (Figures 10, 16). Male tissue intermingled between female acini. Seminal vesicle anterior to gonad, very convoluted, with narrow walls. Common glandular genital duct broad, located on right side of pallial roof, bulging ventrally into haemocoel space; lumen with few longitudinal glandular folds and short cilia. Prostatic gland well differentiated, ventrally located; capsule gland covering outer region of prostatic gland (Figure 18). Genital aperture and penis not observed. Oogonia and oocytes in various degrees of differentiation, randomly distributed (found in two dissected specimens).

Central nervous system: Pair of fused cerebro-pleural ganglia located posterior to buccal bulb; pedal ganglia located ventral to oral tube. Statocyst of about half eye volume, immerse anterior to pedal ganglia into pedal musculature, with a single and relatively large (similar to eye in diameter) statolith (Figure 16).

Type Material: Holotype (MLP 6367) (720 μm in diameter). Paratypes: 9 specimens (MLP 6368), 5 specimens (MZSP 38708 + 9 slides of serial section of 2 specimens), all from the type locality, March 1998.

Type Locality: 54°52′ S, 68°12′ W, Isla H, Beagle Channel, Tierra del Fuego, Argentina.

Distribution: Known only from type locality.

Etymology: The species name derives from Patagonia, region on southern part of South America.

DISCUSSION

Three species of Orbitestellidae were previously reported from the Magellanic Region and adjacent subantarctic waters: *Microdiscula subcanaliculata* (Smith, 1875) from South Georgia Islands and South Orkneys Islands (Ponder, 1983 and 1990), *Microdiscula vanhoffeni* Thiele, 1912, from South Shetlands Islands (Dell, 1990) and *Orbitestella ponderi* from East Beagle Channel and southeastern Pacific Ocean, Chile (Linse, 2002). *Orbitestella ponderi* was also collected during this study along the Beagle Channel at Ushuaia Bay (≈ 54°50′ S, 68° W), Gable Island (54°54.6′ S, 67°21.4′ W) and San Pio Cape (55°5.6′ S, 66°28.8′ W); at Sloggett Bay (55°00′ S, 66°20.6′ W) and Isla de los Estados (54°46′ S, 64°22′ W). These new records confirm that *O. ponderi* is partially sympatric with *O. patagonica.*

Orbitestella patagonica differs from *O. ponderi* Linse, 2002, by having a more depressed shell, with much weaker axial sculpture and rounded aperture. *Orbitestella patagonica* differs from the Antarctic species of *Microdiscula* Thiele (1912) by having a more depressed, spirally ornamented shell. The ratio of the umbilicus/last whorl diameter in *O. patagonica* is similar to that of *M. vanhoffeni* and greater than in *M. subcanaliculata. Orbitestella patagonica* also differs from the Australian and New Zealand congeneric species in having a more rounded shell aperture, more rounded last whorl, and weakly defined commarginal growth lines. *Orbitestella patagonica* also differs from the North Atlantic *O. similis* and *O. cubana* by lacking nodulose sculpture and by having a more rounded last whorl.

The South American species of *Orbitestella* (*O. ponderi* and *O. patagonica*) differ markedly from the Australasian *Orbitestella* species (including the type species) and the North Atlantic species, by having crisp spiral threads covering the entire shell surface, including the protoconch. However, based on jaw morphology and general shell shape, we prefer to expand the generic set of characters for *Orbitestella* instead of a introducing a new generic taxon for the South American species. Beyond these two genera, only *Lurifax* Warén and Bouchet (2001) has also been reported to the family Orbitestellidae (Smriglio and Mariottini, 2002). *Lurifax* is very different from the other genera in having taller spire and multispiral protoconch.

Orbitestella patagonica shows the general anatomical features of the orbitestellids described by Ponder (1990). The main anatomical difference is the proportionally smaller stomach, occupying only the right side of the visceral mass. Radula morphology also show some differences with those previously described and figured by Ponder (1990) as characteristic for *Orbitestella*: the pectinated cutting edge of the rachidian tooth in *O. patagonica* is wider and not as triangular as in *O. wareni* Ponder, 1990; the cutting edge of the lateral teeth were described by Ponder (1990) as a wide plate with numerous small cusps in the outer margin, while in *O. patagonica* they are narrower and having only few cusps; marginal teeth are wide and numerously cusped in the species described by Ponder (1990) and are narrow, hook-like and without additional cusps in *O. patagonica.* The jaws in *O. patagonica* have only five rows of serrated plates, while Ponder (1990) described six and seven rows for the species he studied. Both radula and jaws of *O. patagonica* are similar to those of *O. ponderi.*

Orbitestella patagonica, as it was previously reported for *O. wareni* by Ponder (1990), has the general anatomical features of a basal heterobranch, such as the lack of

ctenidium, the hermaphrodite genital system mostly bulging into the haemocoel, the lack of odontophoral cartilages and the presence of a pigmented mantle gland.

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Sphaeriidae (Bivalvia) from Peruvian Amazon floodplains, with the description of *Pisidium iquito* new species

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ABSTRACT

This article reports on the sphaeriid bivalves collected during a faunistic survey at the Pacaya-Samiria Reserve, in the Peruvian Amazon. A new species of *Pisidium* C. Pfeiffer, 1821, from floodplain habitats, is described. *Pisidium iquito* new species is defined by its large, high, not-inflated shell, with trapezoidal shell outline, beaks prominent, sub-central; the ligament externally visible and tending to be protruded, and the presence of only one branchial opening and one demibranch, are also diagnostic. The presence of *Pisidium sterkianum* Pilsbry, 1897, from small watercourses in the Peruvian Amazon is reported for the first time. *Eupera simoni* (Jousseaume, 1889) is reported from the surveyed area, figured, and compared with other Peruvian and Brazilian species.

INTRODUCTION

As it is the case for large geographic areas of southern South America, knowledge of the molluscan fauna from the Amazonian floodplains is rather poor. Particularly scant is the information from the Peruvian Amazon. More extensive surveys on the molluscan fauna have been done in the Brazilian Amazon (Pain, 1960; Bonetto, 1967, 1972; Paraense, 1967, 1975). Relevant results dealing with the composition of the invertebrate assemblages in Brazilian Amazonian rainforest have also been reported by Dreher-Mansur and Valer (1992) and Volkmer-Ribeiro et al. (1998). Among Bivalves, the sphaeriid fauna of Peru and in particular of the Amazonian floodplains is virtually unknown. Previous literature records account mainly for the sphaeriids from high-altitude environments of the Central Andes (Kuiper and Hinz, 1984). To date, two *Pisidium* species, two species of *Eupera*, and three species of *Sphaerium* have been the only Sphaeriidae reported as living in Peru (Kuiper and Hinz, 1984; Ramírez and Arenas, 2003).

In the present paper, sphaeriids collected during a faunistic survey in a small area of the Peruvian Amazon at the Pacaya-Samiria Reserve, a protected area limited by the Marañón and Ucayalí rivers, are reported, and a new species of *Pisidium* is described.

MATERIALS AND METHODS

Materials for this study were obtained in September 2002, during the low-water period of the Amazon floodplains at the Pacaya-Samiria Reserve, Loreto, Peru (Figure 1). Sphaeriids were collected from stagnant water bodies, the so-called "cochas", flowing watercourses locally called "caños" (both habitats were profusely covered by floating meadows) and from small muddy-bottom streams. The local term "cocha" designates an ancient river branch or meander that, due to high rates of sedimentation, became separated from the main course, forming ponds of variable sizes.

Sphaeriids were relaxed for study by a brief rinsing in warm water (approx. 50°C) and immediately fixed in ethanol 70°. Specimens for scanning electron microscopy were cleaned after dissection of soft parts, with a concentrated solution of sodium hypochlorite, adequately mounted and coated. Linear measurements: shell length (SL), shell height (SH), shell width (SW); shape indices and morphometric ratios: height index (HI = SH/SL), convexity index (Ci = SW/SH), and ratio hinge length (HiL): shell length (HiL/SL), were calculated according to the criteria followed by Ituarte (1996). For each calculation (N = 10), mean and standard deviation values are given.

For comparative purposes, the following type material was examined: syntypes of *Pisidium sterkianum* Pilsbry, 1897, Academy of Natural Sciences, Philadelphia (ANSP) and paratypes of *Pisidium forense* Meier-Brook, 1967, Senckenberg Museum, Frankfurt (SMF), *Eupera klappenbachi* Mansur and Veitenheimer, 1975, Museo de La Plata (MLP), and *Eupera doellojuradoi* Klappenbach, 1962, Museo Argentino de Ciencias Naturales (MACN), were used.

SYSTEMATICS

Pisidium iquito new species
(Figures 2–13)

Description: Shell thin, translucent, large (maximum observed size: 7.2 mm; mean SL of specimens examined:

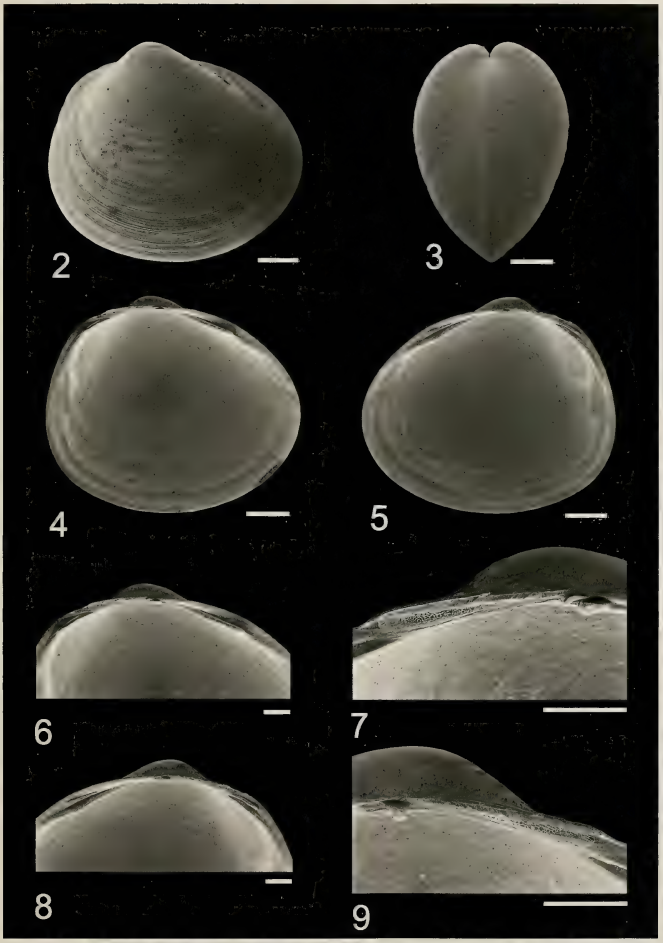
Figure 1. Location map. Encircled area indicates type locality for *Pisidium iquito* new species.

5.4±1.2, n = 10), somewhat high (mean HI = 82±2), not convex (mean Ci = 68 ± 4), shell outline sub-quadrangular, tending to trapezoidal in medium-sized and larger specimens, anterior end produced in a short sharp curve, somewhat pointed, posterior end short, truncated, nearly straight, somewhat oblique (Figures 2, 4, 5, 11); dorsal margin gently curved, short, ventral margin uniformly and markedly curved. Beaks prominent, well raised from shell surface, wide at base, pointed at the tip, somewhat directed backward, well visible but not much projected above dorsal margin, slightly displaced backward, at about 59% of SL. Shell surface finely and irregularly striated, glossy, straw-yellowish.

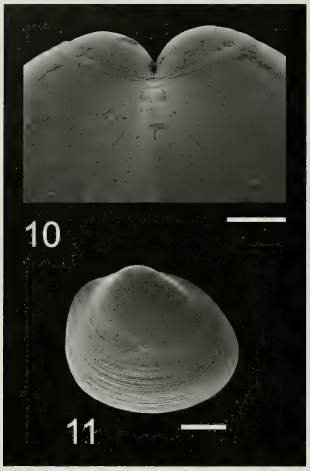
Hinge plate weak, hinge line rather long (HiL/SL about 57%). Hinge: Right valve (Figures 5, 8, 9): cardinal tooth (C_3) narrow and straight at anterior half, curved and enlarged in a slightly sulcated cup at posterior end. Lateral teeth slender, delicate, inner anterior lateral (AI) long, slightly curved, cusp displaced forward; outer anterior lateral tooth (AIII) very short, cusp distal; inner posterior lateral (PI) straight, cusp sub-central; outer posterior lateral (PIII) reduced in size, straight, with distal cusp. Left valve (Figures 4, 6, 7): cardinal teeth well developed, the inner (C_2) robust, blunt, projected below hinge line, slightly bent upward at tip, with base slightly oblique with respect to antero-posterior axis, the outer (C_4) a short, flat, curved lame, with distal part slightly bent upward, quite oblique, overlapping C_3 at posterior half; anterior lateral tooth (AII) slender, straight, cusp well displaced distally; posterior lateral tooth (PII) relatively short, weak, slightly curved, cusp distal.

Ligament pit long and slender, lanceolate, not deep, inner margin slightly sinuous at anterior half, enlarged and uniformly concave at posterior half (Figures 7, 9). Escutcheon long, lanceolate, marked by a delicate line (Figure 10). Ligament external, long (representing about 21% of shell length), delicate, well visible from outside, moderately elevated over dorsal margin or protruded in variable degrees (Figures 7, 9, 10).

Anatomy: Only the anal mantle opening present, a pair of well developed, but not particularly strong, siphonal retractor muscles present (Figure 13). The mantle fusion anterior to anal siphon not long, representing 11 ± 2% of SL (Figure 13). Mantle edge broad. Muscle scars (up to 10 are usually clearly visible) corresponding to the inner radial mantle muscles well-marked, lying well apart from the pallial line (Figure 13), those corresponding to anal siphon retractors are coalescent with posterior adductor muscle scars, the one that would correspond to the absent branchial opening (sr_3) stronger than the remaining (Figure 13) that appear grouped in triads (Figures 4, 5). Only one demibranch, the inner, present.



Figures 2–9. *Pisidium iquito* new species. **2–3.** Holotype (MLP 6859–5). **2.** Right lateral view. **3.** Posterior view. **4–9.** Paratypes (MLP 6859–5). **4.** Left valve, inner view. **5.** Right valve, inner view. **6.** Hinge of left valve. **7.** Left valve, detail of cardinal teeth and ligament. **8.** Hinge of right valve. **9.** Right valve, detail of cardinal tooth and ligament. Scale bars: Figures 2–5 = 1 mm; Figures 6–9 = 500 μm.



Figures 10–11. *Pisidium iquito* new species. Paratypes MLP 6859–5. **10.** Posterior view showing the external ligament. **11.** Lateral view of a medium sized specimen. Scale bars: Figure 10 = 1 mm; Figure 11 = 500μm.

Brood pouches developing upward and posteriorly in each inner demibranch, with up to 24 embryos found in a specimen of 6.5 mm length. Nephridia of closed type, dorsal lobe elongate with lateral loop visible in dorsal and posterior and dorsal views (Figure 12).

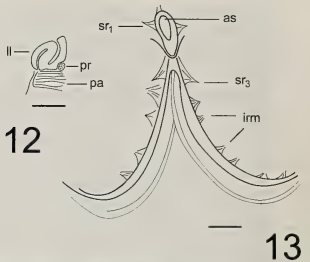
Type Locality: "Cocha" Tamara, 05°16′28″ S, 74°29′55″ W, Pacaya-Samiria Reserve, Department of Loreto, Peru (Figure 1).

Type Material: Holotype, MLP 6859–5; 3 paratypes: 3 MLP 6859–5, 1 MNHN unnumbered.

Other Material Examined: Unnamed small stream (05°16′12″ S, 74°21′27″ W) that flows into the Pacaya River, at the entrance to the Pacaya—Samiria National Reserve (Figure 1), on muddy soft bottoms, 20 specimens, MLP 6863–1–1.

Etymology: The species name refers to the Iquitos, ancient people who inhabited the Peruvian Amazon floodplains.

Remarks: *Pisidium iquito* new species is defined by its large maximum size, being the largest South American species of *Pisidium*, sub-quadrangular shell shape, prominent beaks, markedly weak hinge plate, ligament external, tending to be protruded, and by the presence of only one demibranch, the outer one, nephridia of



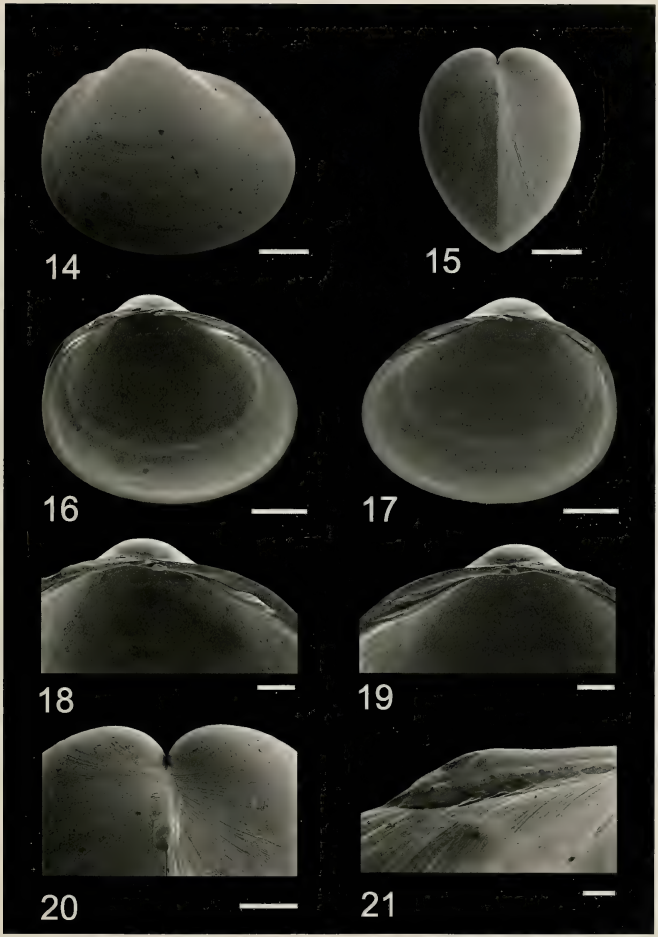
Figures 12–13. *Pisidium iquito* new species. **12.** Nephridium. **13.** Mantle muscles. (**as**: anal siphon; **irm**: inner mantle radial muscles; **pa**: posterior adductor muscle; **pr**: pedal retractor muscle; $\mathbf{sr}_1$: anal siphon retractor muscle; $\mathbf{sr}_3$: retractor muscle corresponding to the position of lacking branchial opening. Scale bars = 1 mm.

closed type, with dorsally visible lateral loop, and only one mantle opening, the anal. *Pisidium iquito* new species and *Pisidium sterkianum* Pilsbry, 1911, have the same the number of demibranchs, mantle openings, and type of nephridia; however, *Pisidium iquito* new species has a less convex and higher sub-quadrangular shell, with more prominent and more centrally located beaks; both species have an external ligament, although much more protruded in *P. sterkianum*. *Pisidium iquito* new species chiefly differs from *Pisidium meierbrooki* Kuiper and Hinz, 1984, from the Peruvian highlands and *Pisidium chiquitanum* Ituarte, 2001, from central Bolivian lowlands in both shell characters (being larger with no ovate shell outline) and soft anatomy (having only one demibranch and one mantle opening). *Pisidium iquito* new species resembles *Pisidium forense* Meier-Brook, 1967, from the southwestern Brazilian drainage basin, having a similar siphonal arrangement and only one pair of demibranchs; however, *Pisidium iquito* new species differs by its larger size, relatively larger height, less convexity, and beaks more displaced backwards. Baker (1930) described several sphaeriids from northern South America, among them *Pisidium bejumae* Baker, 1930, from a savanna pond in Venezuela, which is similar to *Pisidium iquito* new species in having a relatively high shell with centrally located, full, and prominent beaks; however, *P. bejumae* has smaller size, having higher and more convex, with short, ellipsoid, not trapezoidal, shell outline; the ligament also differs, not tending to be protruded as in *P. Iquito* new species.

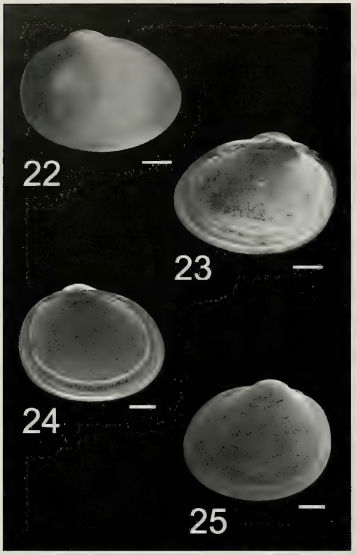
Pisidium sterkianum Pilsbry, 1897
(Figures 14–25)

Pisidium sterkianum Pilsbry, 1897: 291–292, pl. 6, figs. 1–4.

Description: Shell of medium size (maximum ob-



Figures 14–21. *Pisidium sterkianum* Pilsbry, 1897 (MLP 6863–1). **14.** Right lateral view. **15.** Posterior view. **16.** Left valve, inner view. **17.** Right valve, inner view. **18.** Left valve, detail of cardinal teeth and ligament. **19.** Right valve, detail of cardinal tooth and ligament. **20.** Posterior view with detail of external ligament. **21.** Lateral view of posterior end with detail of protruded external ligament. Scale bars: Figures 14–17 = 1 mm; Figures 18–20 = 500 μm; Figure 21 = 100μm.



Figures 22–25. *Pisidium sterkianum* Pilsbry, 1897. **22–23.** Syntypes (ANSP 70490). **22.** Right valve, outer lateral view. **23.** Right valve, inner view. **24–25.** MLP 5061. **24.** Left valve, inner lateral view. **25.** Left valve, outer lateral view. Scale bars: Figures 22–25 = 1 mm.

served SL = 5.7 mm), rather inflated (mean CI = 73±2). Shell outline ovate, somewhat high (mean HI = 82±3); dorsal margin slightly shorter than ventral margin, gently curved; ventral margin evenly and widely curved. Anterior end produced in a somewhat acute curve, posterior end truncated. Beaks wide at base, full, nearly central (located at about 58% of shell length), well visible above dorsal margin. Surface finely and regularly striated.

Hinge plate narrow, not solid. Hinge line long (HiL/S = 63±31). Hinge: Right valve (Figures 17, 19): a minute, somewhat weak, cardinal tooth (C_3), enlarged at posterior end forming a slightly grooved cup; anterior right lateral teeth well-developed, the inner (AI) a long, broadly curved lamella, cusp low, somewhat displaced forward; the outer (AIII) shorter, cusp distal, bent upward. Posterior lateral teeth straight, the inner (PI) narrow, cusp sub-central, the outer (PIII) shorter with cusp distal. Left valve (Figures 16, 18): two well-developed cardinal teeth, the inner (C_2) short, bent upward at tip, the outer (C_4) slightly longer than C_2, slender, evenly arcuate, slightly oblique with respect to antero-posterior axis, overlapping C_2 at posterior half. Anterior (AII) and posterior (PII) lateral teeth well-developed, the anterior stronger, cusps high, triangular, displaced distally. Ligament pit slender, long, not deep. Ligament external, markedly protruded and well visible from the exterior (Figures 20, 21); ligament length about 21% of shell length.

Anatomy: Only the anal mantle opening present; only one, the inner, demibranch present, brood pouch developing from the upper part of inner wall of descending lamella, up to 8 embryos per demibranch were found. Seven weakly marked muscle scars, corresponding to inner radial mantle muscles, located slightly above the pallial line, each bundle formed by few weak muscle fibers. Nephridia of closed type, with lateral loop visible in posterior view.

Type Locality: From a creek in the "Prado" (actually corresponding to Arroyo Miguelete), Montevideo, Uruguay.

Material Examined: Unnamed small stream (05°16′12″ S, 74°21′27″ W) that flows into the Pacaya River, at the entrance to the Pacaya-Samiria National Reserve (Figure 1), on muddy soft bottoms; 27 syntypes ANSP 70490; > 50 specimens, Arroyo Miguelín (a small watercourse flowing into the Río de La Plata), Ensenada Buenos Aires, Argentina, MLP 5061.

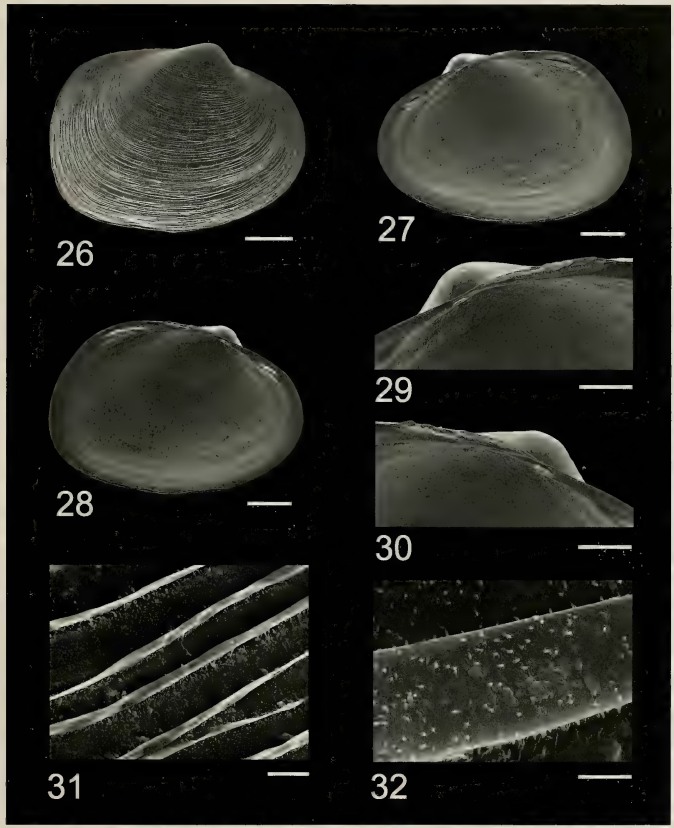
Remarks: Diagnostic characters of *Pisidium sterkianum* are: shell rather solid, medium-sized, inflated, beaks wide, sub-central; ovate shell outline, expanded forward, ligament external and protruding, only exhalant mantle opening and only inner demibranch, present; nephridia of closed type, with lateral loop visible from dorsal view.

When compared with the syntypes of *Pisidium sterkianum* (ANSP 70490) (Figures 22, 23) and specimens from the Río de La Plata, Argentina (MLP 5061) (Figures 24, 25), the general shell shape of Amazonian specimens is somewhat higher, the shell outline is less oval with posterior end consistently higher, markedly truncated, and beaks are more outstanding from shell surface.

Eupera simoni (Jousseaume, 1889)
(Figures 26–32)

Limosina simoni Jousseaume, 1889: 217, pl. 9, figs. 22, 23
Eupera simoni Klappenbach, 1967:110; Dreher Mansur and Valer, 1992: 94; Dreher-Mansur and Meier-Brook, 2000: 5.

Description: Shell medium to large (maximum observed SL = 8 mm), relatively low (mean HI = 71±2), not inflated (mean Ci = 70±5), shell outline moderately oval, posterior end truncate, slightly curved, oblique in larger specimens, anterior end evenly rounded, not pointing (Figures 26–28). Dorsal margin slightly and evenly arcuate, ventral margin widely curved. Beaks triangular, pointed, well marked-off from shell surface, but



Figures 26–32. *Eupera simoni* (Jousseaume, 1889). **26.** MLP 6859–6. Right valve, outer lateral view. **27–30.** MLP 6864–1. **27.** Right valve, inner lateral view. **28.** Left valve, inner lateral view. **29.** Right valve, detail of cardinal tooth and ligament. **30.** Left valve, detail of cardinal tooth and ligament. **31.** Periostracum folds. **32.** Detail of periostracum folds and papillae. Scale bars: Figures 26–28 = 1 mm; Figures 29, 30 = 500μm; Figure 31 = 25 μm; Figure 32 = 5 μm.

not prominent, somewhat directed forward; located at about 33 % of shell length (Figures 26–28).

Hinge plate weak, extremely narrow below beaks, hinge line relatively long (HiL/SL about 60%). Hinge: Right valve (Figures 27, 29): cardinal tooth (C_3) weak, a straight, narrow blade, very close to ventral margin of hinge plate; anterior lateral teeth short, the inner (AI) robust, cusp sub-central, the outer (AIII) quite reduced in size; posterior lateral teeth (PI and PIII) delicate, slender, almost straight. Left valve (Figures 28, 30): cardinal tooth ($C_{2?}$) minute, not very high, anterior (AII) and posterior (PII) lateral teeth relatively low, slightly

curve, cusps sub-central in AII, nearly distal in PII. Inner shell surface with spots of dark pigment sparsely distributed in small groups, two larger pigmented areas above and below scar of posterior adductor muscle, usually present. Periostracum thin, forming commarginal folds, periostracum surface entirely covered by very small papillae, up to 0.5 μm long, distributed without a definite pattern (Figures 26, 31, 32).

Anatomy: The general anatomy fits into the generic diagnosis. Worth mentioning is a somewhat marked development of the posterior foot retractor muscle, whose insertion point is well marked just over the scar corresponding to the posterior adductor muscle. Up to 18 embryos were found within each maternal demibranch.

Type Locality: Laguna de Espino, Caracas, Venezuela.

Material Examined: Pacaya-Samiria Reserve (Figure 1): Cocha Tamara, 05°16′28″ S, 74°29′55″ W (MLP 6859–6); Cocha Yarina, 05°24′42″ S, 74°30′23″ W (MLP 6865–1), attached to roots of *Eichornia* sp.; Pacaya River, 5°16′55″ S, 74°25′45″ W (MLP 6886–1), on roots of floating meadows; Caño Yarina, 05°21′28″ S, 74°30′29″ W (MLP 6864–1).

Remarks: *Eupera simoni,* a common species in the Peruvian Amazon, is easily identified by the somewhat shortened shell outline due to the posterior truncated margin, beaks small, pointed, relatively low but well discernible from shell surface, and periostracum raised in well-defined commarginal folds. *Eupera primei* Klappenbach, 1967, described from water courses close to the Ucayalí River, Peru, not far from Pacaya-Samiria Reserve, differs from *E. primei* in having a higher shell, with shell outline tending to be circular, dorsal margin strikingly curved, and very low periostracal folds. *Eupera klappenbachi* Mansur and Veitenheimer, 1975, a species common in western Brazilian drainages, is similar to *E. simoni,* consistently differing in being higher and more convex, and having more prominent and pointed beaks; *Eupera platensis* Doello Jurado, 1921, from the Río de La Plata has a more solid shell, with more centrally located beaks, stronger cardinal teeth and robust laterals. *Eupera simoni* is quite different from *Eupera guaraniana* Ituarte, 1994, from the Uruguay River, a large species with a striking trapezoidal shell outline, and also differs from *Eupera elliptica* Ituarte and Mansur, 1993, from the Iguazú River, Northern Argentina, a species characterized by its strikingly elliptic shell outline. *Eupera guaraniana* and *E. elliptica* also differ from *E. simoni* in having two types of periostracal papillae, the larger ordered in radial rows.

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Note

Dates of publication of Yoichiro Hirase's *Kai Chigusa*

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Yoichiro Hirase (1859–1925) set himself up in business from 1887 as a shell dealer in Kyoto, Japan. Over the following 33 years, he built one of the world's first shell museums and produced and published the 'Conchological Magazine' together with a number of books on the Mollusca. Perhaps the best known among the latter is *Kai Chigusa*, a title often erroneously cited as *Kai Sen Shu*. *Sen shu* is the nominal Japanese reading of the Kanji characters for 'thousand' and 'kinds', but *Chigusa* is a classical reading that is admittedly unfamiliar even to many modern-day Japanese. Hirase studied Chinese classics in his youth, however, and frequently used classical or poetic readings of Kanji characters.

Published between 1914 and 1922, *Kai Chigusa* was a four-volume work that portrayed 400 predominantly Japanese mollusks in hand-colored woodblock prints. It was bound in the traditional Japanese 'concertina' style. Ten volumes were originally planned, depicting a total of 1000 species (whence the English title, 'The illustrations of a thousand shells'), but straitened economic circumstances forced a downsizing of the project after 1915 (Callomon and Tada, in prep).

A collation of the work was provided by Higo et al. (1999: 581). Four new species were figured and named in it: *Mandarina omphalina* Hirase, 1915, *Calliostoma akoya* Hirase, 1922, *Gaza (?) nobilis* Hirase, 1922 and *Fulgoraria kaneko* Hirase, 1922. Complete sets of all four volumes are relatively rare, and cognoscenti have long suspected that the more common earlier volumes were printed in larger numbers than the later ones.

The author recently came across a collection of correspondence between Alvin R. Cahn and R. Tucker Abbott of the Academy of Natural Sciences of Philadelphia (ANSP) that spans the years 1947–1968. Cahn was a fisheries scientist who worked for the Natural Resources Division of Supreme Headquarters Allied Forces in Tokyo for several years from 1947. His work brought him into contact with many of the leading Japanese marine scientists of the day, including Tokubei Kuroda (1886–1987), Hirase's one-time assistant and museum manager. During a long stay in Japan, Cahn built up an extensive library and a collection of mollusk specimens, both of which were donated in a series of gifts to the ANSP that started in 1957. His library included a fine complete set of *Kai Chigusa*, together with some notes he had made regarding the production of this work. In 1955, Cahn wrote to the Unsodo company, the publishers of *Kai Chigusa*, requesting information about its publication. After a long wait he received a noncommittal reply. In August 1957 he invoked his authority as a former representative of the occupation forces to press Unsodo's president, Mr Shigeji Yamada, for information. Yamada replied on September 7th of that year with a full account compiled from company records. This has apparently

Figure 1. Cover of the first volume (1914) of *Kai Chigusa*.

Table 1. Dates of publication and press runs of *Kai Chigusa*.

Volume 1		
First printing	300 copies	May 1, 1914
Second printing	100 copies	December 24, 1914
Third printing	100 copies	January 17, 1917
Fourth printing	100 copies	September 6, 1919
Fifth printing	100 copies	August 17, 1921
Sixth printing	100 copies	April 2, 1925
Seventh printing	50 copies	June 12, 1930
Eighth printing	30 copies	March 28, 1937
Total:	880 copies	
Volume 2		
First printing	300 copies	January 10, 1915
Second printing	100 copies	August 22, 1917
Third printing	100 copies	September 6, 1919
Fourth printing	100 copies	February 28, 1922
Fifth printing	100 copies	February 21, 1926
Sixth printing	50 copies	March 13, 1935
Total:	750 copies	
Volume 3		
First printing	300 copies	November 10, 1915
Second printing	100 copies	September 6, 1919
Third printing	100 copies	July 28, 1922
Fourth printing	100 copies	February 21, 1926
Fifth printing	50 copies	November 20, 1933
Total:	650 copies	
Volume 4		
First printing	300 copies	January 15, 1922
Second printing	50 copies	October 26, 1929
Third printing	50 copies	March 13, 1935
Total:	400 copies	

never been published, and the main information is reproduced here. Interestingly, Yamada also used the erroneous reading *Kai Sen Shu*.

From the figures provided to Cahn, it is clear that demand for *Kai Chigusa* persisted long after its author's death in 1925. Nevertheless, the suspicion that the number of copies printed of each volume varies is clearly

Figure 2. A plate from the first volume (1914) of *Kai Chigusa*.

grounded in fact. There are more than twice as many copies of the first volume than of the last. Yamada confirmed that despite *Kai Chigusa*'s long life in print, the date of printing given in the colophon was never changed. It is thus not possible to determine which printing any given copy represents.

In a letter of April 27, 1957 Cahn told R. Tucker Abbott: 'Incidentally, all the original woodblock plates are still intact; I have seen them. They probably number well into the thousands, there being often as many as a dozen or more for a single shell print: they occupy an entire room from the floor to the ceiling'. A representative of Unsodo has recently confirmed that the blocks continue to exist, though reassembling the plates for printing would now involve prohibitive expense.

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AUTHOR INDEX

Ardila, N. E. 131
Bennett, D. J. 127
Calado, G. 129
Callomon, P. 175
Cazzaniga, N. J. 71
Coles, B. 55
Cowie, R. H. 52, 71
Davis, E. C. 127
Duerr, R. 152
Filún, M. 121
Gallardo, C. S. 121
García, F. J. 139, 144
Glaubrecht, M. 71
González-Wangüemert, M. 103
Groves, L. T. 43
Harasewych, M. G. 1, 93
Herbert, G. S. 157
Ituarte, C. 167
Kantor, Y. I. 1
Manque, C. 121
Nielsen, S. V. 88
Ortiz, A. 103
Pérez, K. E. 127
Pérez-Ruzafa, A. 103
Rosique, M. J. 103
Simone, L. R. L. 160
Slapcinsky, J. 55
Troncoso, J. S. 139
Urgorri, V. 144
Valdés, Á. 131
Vermeij, G. J. 157
Zalvide, P. C. 144
Zelaya, D. G. 112, 160

NEW TAXA PROPOSED IN VOLUME 118 (2004)

GASTROPODA

Anetarca brasiliana García and Troncoso, 2004, new species (Facelinidae) 139
Armina elongata Ardila and Valdés, 2004, new species (Arminidae) 136
Bernaya (Bernaya) beardi Groves, 2004, new species (Cypraeidae) 47
Bernaya (Bernaya) jeanae Groves, 2004, new species (Cypraeidae) 46
Bernaya (Protocypraea) popenoei Groves, 2004, new species (Cypraeidae) 47
Cirsotrema cirritum Duerr, 2004, new species (Epitoniidae) 154
Coluzea kallistropha Harasewych, 2004, new species (Turbinellidae) 93
Coluzea madagascarensis Harasewych, 2004, new species (Turbinellidae) 95
Coluzea naxa Harasewych, 2004, new species (Turbinellidae) 100
Columbarium quadrativaricosum Harasewych, 2004, new species (Turbinellidae) 98
Drepanodontus Harasewych and Kantor, 2004, new genus (Buccinulidae) 7
Drepanodontus tatyanae Harasewych and Kantor, 2004, new species (Buccinulidae) 7
Germonea Harasewych and Kantor, 2004, new genus (Buccinulidae) 20
Germonea rachelae Harasewych and Kantor, 2004, new species (Buccinulidae) 20
Lusitromina Harasewych and Kantor, 2004, new genus (Buccinulidae) 25
Muffinbuccinum Harasewych and Kantor, 2004, new genus (Buccinulidae) 13
Muffinbuccinum catherinae Harasewych and Kantor, 2004, new species (Buccinulidae) 14
Olivancillaria matanzana Nielsen, 2004, new species (Olividae) 90
Orbitestella patagonica Simone and Zelaya, 2004, new species (Orbitestellidae) 161
Palaeocypraea (Palaeocypraea) wilfredi Groves, 2004, new species (Cypraeidae) 45
Pilsbryna nodopalma Slapcinsky and Coles, 2004, new species (Gastrodontidae) 61
Pilsbryna quadrilamellata Slapcinsky and Coles, 2004, new species (Gastrodontidae) 63
Spikebuccinum Harasewych and Kantor, 2004, new genus (Buccinulidae) 2
Spikebuccinum stephaniae Harasewych and Kantor, 2004, new species (Buccinulidae) 2
Stramonita penelaevis Vermeij and Herbert, 2004, new species (Muricidae) 157

POLYPLACOPHORA

Leptochiton (Leptochiton) troncosoi Zalvide et al., 2004, new species (Leptochitonidae) 144
Leptochiton (Leptochiton) pepezamorai Zalvide et al., 2004, new species (Leptochitonidae) 147

BIVALVIA

Pisidium iquito Ituarte, 2004, new species (Sphaeriidae) 167

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CONTENTS

Kevin J. Roe
Paul D. Hartfield
Hamiota, a new genus of freshwater mussel (Bivalvia: Unionidae) from the Gulf of Mexico drainages of the southeastern United States 1

Russell L. Minton
Steven P. Savarese, Jr.
Consideration of genetic relationships in management decisions for the endangered Anthony's riversnail, *Leptoxis crassa anthonyi* (Redfield, 1854) (Gastropoda: Pleuroceridae) 11

Frank Köhler
Matthias Glaubrecht
Fallen into oblivion—the systematic affinities of the enigmatic *Sulcospira* Troschel, 1858 (Cerithioidea: Pachychilidae), a genus of viviparous freshwater gastropods from Java 15

John Slapcinsky
Six new species of *Paryphantopsis* (Gastropoda: Pulmonata: Charopidae) from the Papuan Peninsula of New Guinea 27

Ángel Valdés
Kelvin Barwick
First record of *Akera* Müller, 1776, from the eastern Pacific, with the description of a new species 43

Claude Vilvens
Description of *Calliotropis pulvinaris* new species (Gastropoda: Trochidae: Eucyclinae: Calliotropini) from West Madagascar 50

Notice 54

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Hamiota, a new genus of freshwater mussel (Bivalvia: Unionidae) from the Gulf of Mexico drainages of the southeastern United States

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ABSTRACT

Hamiota, a new genus of freshwater mussel containing four species formerly assigned to the genus *Lampsilis* Rafinesque, 1820, is described. In addition to the genus *Lampsilis*, members of *Hamiota* had previously been placed in the genera *Villosa* Frierson, 1927, and *Ligumia* Swainson, 1840. Several characters including the packaging of their larvae in a superconglutinate lure to attract host fishes, placement and shape of the marsupia, and release of glochidia through the excurrent siphon, support the recognition of these species as a distinct genus.

INTRODUCTION

Following the discovery in 1988 by Robert Butler of the first superconglutinate lure ensnared on a snag in a tributary of the Choctawhatchee River, a number of publications (e.g., Haag et al., 1995; Hartfield and Butler, 1997; O'Brien and Brim Box, 1999; Blalock-Herod et al., 2002) have confirmed through direct observation the supposition that these unique lures are produced by four species of freshwater mussels endemic to the Gulf of Mexico drainages of the southeastern United States. Herein, we confirm earlier published suggestions that these four species represent a distinct genus of freshwater mussels (Fuller and Bereza, 1973; O'Brien and Brim Box, 1999). The recognition of this genus is based on several characters including the production of the superconglutinate lure, and the unique shape and placement of the marsupia (the region of the demibranchs where female unionoid mussels brood developing larvae), and is supported by molecular evidence (Roe et al., 2001). Use of marsupial features is consistent with previous designations of unionid "divisions" initiated by Simpson (1900a) and continued by Heard and Guckert (1970). The designation of *Hamiota* increases the number of North American unionids genera to 50 (Turgeon et al., 1998).

MATERIALS AND METHODS

A list of specimens examined is included in Appendix 1. Acronyms used in the text are: Academy of Natural Sciences of Philadelphia (ANSP), Delaware Museum of Natural History (DMNH), Florida Museum of Natural History (UF), United States National Museum (USNM), University of Alabama Unionid Collection (UAUC), and Mississippi Museum of Natural Science (MMNS). Abbreviated synonymies are presented for each taxon and include novel combinations and publications with illustration. Measurements were taken to the nearest 0.05 mm using dial calipers.

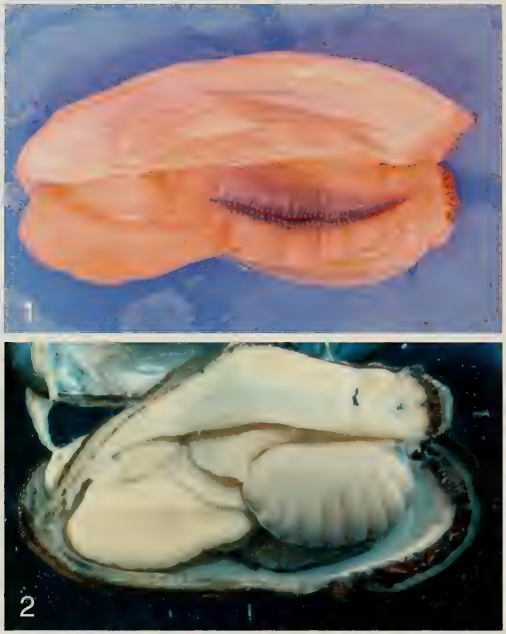
SYSTEMATICS

Family Unionidae Rafinesque, 1820
Tribe Lampsilini von Ihering, 1901

Hamiota new genus. Type species: *Hamiota subangulata* (Lea, 1840) by original designation

Diagnosis: A monophyletic group of freshwater bivalves (Roe et al., 2001) in which all of the glochidia are released simultaneously encased in mucous packages that are referred to as superconglutinates (Haag et al., 1995, fig. 1). The superconglutinate lure exits the mantle cavity via the excurrent opening and is encased within a transparent mucous tube (Hartfield and Butler, 1997; O'Brien and Brim Box, 1999). When acted upon by water currents the superconglutinate mimics the movements of a swimming fish, and has been shown to elicit attacks from fishes (Haag and Warren, 1999). The marsupium is restricted to the ventral portion of the outer demibranchs of female mussels (Figure 1). The precise shape and pigmentation of the marsupia, as well as the degree of posterior mantle margin development, varies across species.

Description: Members of this genus are small- to medium-sized freshwater bivalves, and adult valves generally are between 45–100 mm in length. Shells range from ovate to elliptical in outline, and are somewhat



Figures 1, 2. Inner mantle and outer demibranchs of gravid superconglutinate-producing mussels in the genus *Hamiota* and inner mantle and outer demibranchs typical of non-superconglutinate-producing mussels of the genera *Lampsilis, Ligumia,* and *Villosa.* **1.** Female *Hamiota australis.* **2.** Female *Villosa vibex.*

compressed to moderately inflated. Shell thickness ranges from heavy to thin. Sexes display some degree of dimorphism in shell shape. Shells of male mussels are typically more acutely pointed posteriorly, whereas shells of female mussels display an expanded posterior margin. Periostracum is typically smooth, but can be very glossy in some species. Background color ranges from dark-brown and black through chestnut-brown to straw-yellow. Black to bright green rays of variable width are often present and may be limited to the posterior slope, or cover the entire disk. Nacre color is typically white although other colors such as salmon or blue may be seen as well, particularly in the beak cavities or the posterior margins. The marsupia are often asymmetrical in shape; the anterior portion is typically broadest, tapering toward the posterior end. The ventral margin of the marsupium is darkly pigmented in gravid females. Pigmentation of marsupia varies across species and populations and colors may include purple, red, black, or white. In females, the mantle margins anterior to the branchial opening are elaborated to varying degrees. The morphology of the glochidial valves of members of *Hamiota* is similar to that of members of *Lampsilis* or *Villosa* (O'Brien and Brim Box, 1999).

Etymology: *Hamiota* = angler. Derived from the Greek word *hamus,* meaning hook. This name refers to the means by which members of this genus attract host fishes by packaging their parasitic larvae in a lure that mimics a small fish.

Remarks: Species of *Hamiota* generally have been treated as *Lampsilis* due to the similarity in shape and coloration of their shells. Some authors also have included these species in the genus *Villosa* or *Ligumia,* due to shell shape, thickness, and/or ornamentation of the mantle flap. The shells of *Hamiota* species are in-

deed similar to the shells of these genera, and the mantle flap may exhibit characters of both *Lampsilis* and *Villosa*. However, in *Hamiota*, the marsupia is restricted to the ventral half of the posterior portion of the outer demibranchs, while in *Lampsilis*, *Ligumia*, and *Villosa* the marsupium fully occupies the water tubes of the posterior portion of the outer demibranchs (Figure 1). Unlike members of *Lampsilis*, which release larvae through pores in the ventral edge of the demibranchs, members of *Hamiota* release the superconglutinate lure through the excurrent opening. The placement and shape of the marsupium and the extraordinary method of glochidial release and host fish attraction, the superconglutinate, are uniquely derived characters in the Lampsilini that warrant genus-level recognition.

Hamiota altilis (Conrad, 1834) new combination

Unio altilis Conrad, 1834; Conrad, 1834: 43, pl. 2, fig. 1; Chenu, 1845: 21, pl. 1, fig. 1; Reeve, 1865: pl. 23, fig. 109.
Margarita (*Unio*) *altilis* (Conrad, 1834); Lea, 1836: 24.
Margaron (*Unio*) *altilis* (Conrad, 1834); Lea, 1852a: 27.
Lampsilis altilis (Conrad, 1834); Simpson, 1900a: 529; Parmalee and Bogan, 1998: 125, pl. 47.
Unio clarkianus Lea, 1852; Lea, 1852b: 251; Lea, 1852c: 273, pl. 21, fig. 30; Lea, 1852d: 29, pl. 21, fig. 30.
Margaron (*Unio*) *clarkianus* (Lea, 1852); Lea, 1852a: 27.
Lampsilis clarkianus (Lea, 1852); Simpson, 1900a: 532.
Unio gerhardtii Lea, 1862; Lea, 1862a: 168; Lea, 1862b: 208, pl. 31, fig. 277; Lea, 1862c: 30, pl. 31, fig. 277.
Margaron (*Unio*) *gerhardtii* (Lea, 1862); Lea, 1870: 35.
Lampsilis (*Lampsilis*) *gerhardtii* (Lea, 1862); Simpson, 1900a: 532.
Unio doliaris Lea, 1865; Lea, 1865: 88; Lea, 1868: 260, pl. 32, fig. 75; Lea, 1869: 20, pl. 32, fig. 75.
Margaron (*Unio*) *doliaris* (Lea, 1865); Lea, 1870: 42.
Lampsilis (*Lampsilis*) *doliaris* (Lea, 1865); Simpson, 1900a: 533.

Description: Described by Conrad (1834) as sub-oval, thin, and inflated. The periostracum was described as "rugose" and "blackish" with rays and "numerous short vermicular lines on the posterior slope," and the nacre as whitish and iridescent. The periostracum of specimens of *H. altilis* is typically brown to chestnut-brown in color with a variable number of dark green rays. The left valve has two heavy, spatulate pseudocardinal teeth, the smaller above the larger. The right valve has two nearly equally sized triangular teeth, the larger anterior to the smaller. The lateral teeth are short but blade-like, two in the right valve, and one in the left.

The posterior mantle margin of the female is expanded into a well-developed flap with papillae along the border. Coloration, number, and size of papillae vary somewhat between populations. In general, however, the interior mantle flap is colored red to dark red or brown with darker spots, while the exterior of the flap is brown to black, often with vertical lighter bars, and with a small, but prominent dark "eye spot" on the posterior end. Small papillae are present along the mantle flap, usually becoming more robust anteriorly. In males, the mantle flap is typically not expanded and is reddish in color. Marsupia of *H. altilis* are finely tapered at each end when immature, becoming broadly rounded on the ends in most populations, tapering anteriorly in others. Marsupia color is a dark reddish-brown or black along the margin and white above. The anus is usually pigmented red and the incurrent and excurrent siphons are reddish-brown to black. The glochidia of *H. altilis* are described by Haag et al. (1999).

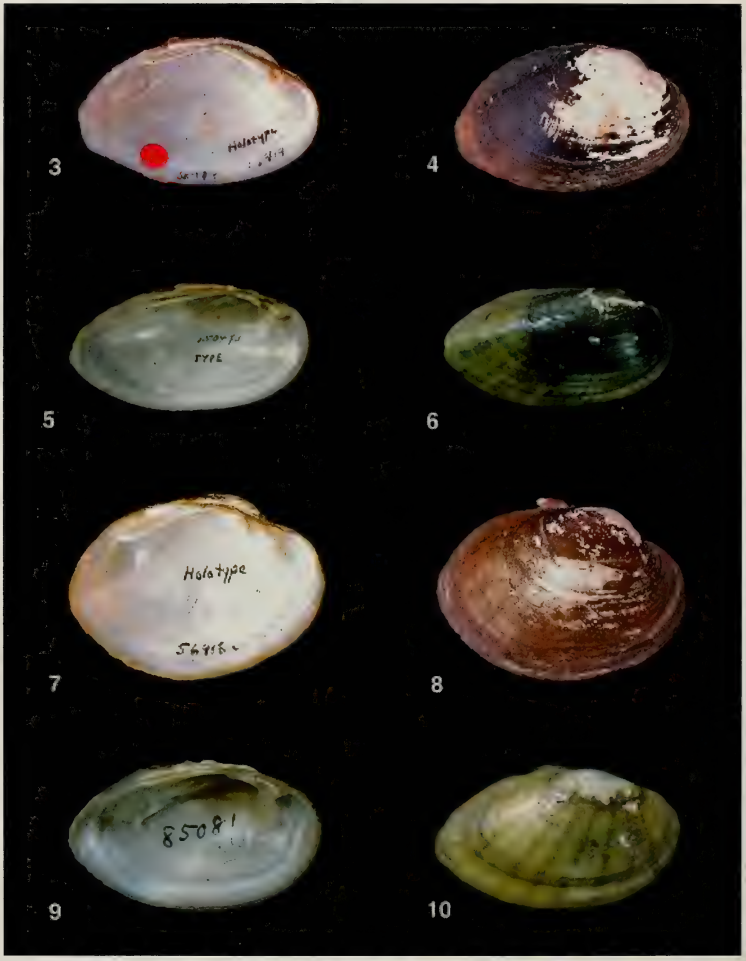
Type Material: *Unio altilis* Conrad, 1834, Lectotype ANSP 56419 (Figures 3, 4) here designated. Type locality: Alabama River, near Claiborne [Monroe Co., Alabama].
Unio clarkianus Lea, 1852, Type not found. Type locality: Williamsport, [Maury Co.], Tennessee; Georgia or Alabama.
Unio doliaris Lea, 1865, Lectotype USNM 84936, here designated. Type locality: Etowah River, Georgia.
Unio gerhardtii Lea, 1862, Holotype USNM 25711 by monotypy. Type locality: Chattanooga, Georgia.

Remarks: The most variable species included in *Hamiota, H. altilis,* is endemic to the Mobile River Basin. Some of the conchological variation is undoubtedly ecophenotypic in nature, although the extent and nature of the variation in shell shape and pigmentation has not been adequately explored.

Conrad (1834) in his original description did not identify a primary type. Johnson and Baker (1973) identified ANSP 56419 as the figured holotype, although the specimen label indicates the locality as "Ogeechee R., Ga." Johnson and Baker (1973) state that the label is in error, and "probably was mixed with ANSP 46418, which is labeled 'Claiborne, Alabama', by error." Conrad (1834) clearly indicated that the specimen(s) of *U. altilis* described were collected from the "Alabama River, near Claiborne." Conrad (1834) did not specifically designate a holotype and according to the ICZN recommendation 73F and Article 74.5 the holotype designation of Johnson and Baker (1973) is deemed invalid. In order to preserve stability of nomenclature, we herein designate specimen ANSP 56419 as the lectotype of *U. altilis*. In accordance with ICZN Article 74.7, we herein designate the specimen USNM 84936 as the lectotype of *U. doliaris* Lea in order to maintain taxonomic stability and because this specimen appears to be that figured by Lea (1868). *Hamiota altilis* is considered threatened by the United States Fish and Wildlife Service (USFWS, 1994).

Life History: Mature gravid females have been reported from March through June. *Hamiota altilis* have also been observed releasing glochidia in a superconglutinate (Haag et al., 1999). Large centrarchid fishes, including *Micropterus coosae* Hubbs and Bailey, 1940, *M. punctulatus* (Rafinesque, 1819), *M. salmoides* (Lacepéde, 1802), and *Lepomis cyanellus* Rafinesque, 1819, have been confirmed as suitable hosts (Haag et al., 1999).

Range: *Hamiota altilis* was historically reported



Figures 3–10. Type material of species of *Hamiota*. Photographs are of the interior of left valve and exterior of right valve. **3, 4.** Lectotype of *H. altilis* ANSP 56419. **5, 6.** Holotype of *H. australis* USNM 150473. **7, 8.** Lectotype of *H. perovalis* ANSP 56416. **9, 10.** Lectotype of *H. subangulata* USNM 85801.

throughout the Mobile River Basin, including the Tombigbee, Black Warrior, Cahaba, Alabama, Tallapoosa, and Coosa River drainages in Alabama, Georgia, Mississippi, and Tennessee. The species is currently restricted to localized portions of the Cahaba, Coosa, and Tallapoosa rivers and some of their tributaries (USFWS, 2003).

Hamiota perovalis (Conrad, 1834) new combination

Unio perovalis Conrad, 1834; Conrad, 1834: 43, pl. 2, fig. 2; Chenu, 1845: 21, pl. 1, fig. 2; Küster, 1861: 257, pl. 87, fig. 2; Reeve, 1866: pl. 38, fig. 209.
Margarita (Unio) perovalis (Conrad, 1834); Lea, 1836: 24.
Margaron (Unio) perovalis (Conrad, 1834); Lea, 1852a: 27.
Lampsilis perovalis (Conrad, 1834); Simpson, 1900a: 531.
Unio spillmanii Lea, 1861; Lea, 1861: 39, Lea, 1862d: 98, pl. 15, fig. 246; Lea, 1862e: 102, pl. 15, fig. 246, Reeve, 1868: pl. 82, fig. 435.
Margaron (Unio) spillmanii (Lea, 1861); Lea, 1870: 42.
Lampsilis (Lampsilis) spillmani (Lea, 1861); Frierson, 1927: 69 [misspelling].

Description: Conrad (1834) described this species as oval and inflated with a moderately thick shell. He noted two color varieties, one in which the periostracum was olivaceous and obscurely rayed with white nacre and another in which the periostracum was reddish-brown with "rose colored" nacre. The periostracum of specimens of *H. perovalis* is generally lighter in color than *H. altilis* and range from straw-yellow to light brown. The number of rays is variable and can cover the entire disk. The left valve contains two robust equal sized pseudocardinal teeth. The right valve has two pseudocardinals and the anterior tooth is smaller than the posterior tooth. The lateral teeth are elongate, two in the left, one in the right.

The mantle margins of female *H. perovalis* are expanded into well-developed flaps, pigmented red on the interior and darker red to brown or black on the exterior. No eyespot is present and short papillae are present along the mantle edge. Males possess a rudimentary mantle margin with weak pigmentation and few papillae. The marsupia of *H. perovalis* are pisciform in shape, broader anteriorly and narrowly tapering posteriorly. The marsupium is reddish or darker along the margin, often with a darker spot of pigment on the broader anterior end that resembles an eyespot in the superconglutinate lure. The anus can be pigmented red and black, and the incurrent and excurrent siphons are usually reddish or brown in color.

Type Material: *Unio perovalis* Conrad, 1834, Lectotype ANSP 56416 (Figures 7, 8), here designated. Type locality: Alabama River, at Claiborne [Monroe Co., Alabama].
Unio spillmanii Lea, 1861, Lectotype USNM 84925, here designated. Type locality: Luxpalila Creek, near Columbus, Mississippi.

Remarks: There has been some question as to the distinctiveness of *H. perovalis* from *H. altilis,* perhaps because both were described from practically the same locality. An examination of mitochondrial DNA sequences by Roe et al. (2001) recovered these two taxa as a clade, but failed to resolve them into reciprocally monophyletic groups. Hurd (1974) considered *perovalis* a junior synonym of *altilis,* as did Burch (1975). Frierson (1927) considered *U. doliaris* (Lea, 1865) a synonym of *perovalis,* although Parmalee and Bogan (1998) include *U. doliaris* as a synonym of *altilis.* Based on the collection locality and the appearance of the type specimen, we place *U. spillmanii* Lea, 1861 as a synonym of *H. perovalis.* As with *U. altilis,* Conrad (1834) did not specifically designate a holotype for *U. perovalis,* therefore, according to the ICZN Article 74.5 and recommendation 73F the holotype designation of Johnson and Baker (1973) is deemed to be in error. In an effort to maintain nomenclatural stability we herein designate ANSP 56419 the lectotype for *U. perovalis.* According to ICZN Article 74.7, the specimen USNM 84925 is here designated as the lectotype of *U. spilmanii* in order to fix the name and maintain nomenclatural stability. This species is listed as threatened by the United States Fish and Wildlife Service (USFWS, 1994).

Life History: Discharge of superconglutinates was first observed in *H. perovalis* (Haag et al., 1995). Glochidia mature and are discharged between March and June, with releases concentrated in early April (Hartfield and Butler, 1997). *Micropterus coosae, M. punctulatus,* and *M. salmoides* have been identified as suitable host fishes for the orange-nacre mucket (Haag and Warren, 1999).

Range: *Hamiota perovalis* was historically known from the Mobile Basin's Alabama, Tombigbee, Black Warrior, and Cahaba rivers and their tributaries in Alabama and Mississippi. The species has apparently become extirpated from the main channels of the larger rivers, but continues to survive in some tributaries of all four drainages (USFWS, 2003).

Hamiota subangulata (Lea, 1840) new combination

Unio subangulatus Lea, 1840; Lea, 1840: 287; Lea, 1842a: 209, pl. 13, fig. 23; Lea, 1842b: 47, pl. 8, fig. 23; Küster, 1861: 278, pl. 94, fig. 2; Simpson, 1892: 415, pl. 58, fig. 1; Reeve, 1868: pl. 65, fig. 327.
Margaron (Unio) subangulatus (Lea, 1840); Lea, 1852a: 29.
Lampsilis subangulatus (Lea, 1840); Simpson, 1900a: 556; Clench and Turner, 1956: 196, pl. 2, fig. 2.
Ligumia subangulata (Lea, 1840); Haas, 1969: 443.
Villosa subangulata (Lea, 1840); Heard, 1979: 44.
Unio kirklandianus S. H. Wright, 1897; S. H. Wright, 1897: 136.
Lampsilis kirklandianus (S. H. Wright, 1897); Simpson, 1900a: 557; Simpson, 1900b: 76, pl. 1, fig. 7.

Description: A medium-sized mussel that reaches approximately 85 mm in length (Brim Box and Williams, 2000). Specimens are generally elongate; the posterior ridge is rounded and the posterior slope is usually con-

cave. Periostracum color is variable in this species. Individuals range from straw-yellow to chestnut-brown in color with a variable number of black to bright emerald green rays of variable width. These rays emanate from the umbo and radiate across the disk. Most shells are shiny, although some populations exhibit an extremely glossy periostracum. This species has been described as one of the most beautiful of all North American freshwater mussels (S. H. Wright, 1897; Clench and Turner, 1956).

Wright (1897) described *U. kirklandianus* from the Ochlockonee River in Leon County, Florida and remarked that his specimens were more polished and had broader rays than typical of *U. subangulatus*, and that the shells were "deeper and broader." The right valve has two somewhat spatulate pseudocardinal teeth, the smaller nearly directly above the other. The left valve has two pseudocardinal teeth, the anterior one much larger than the other. Lateral teeth are thin, but not delicate, two in the left and one in the right valve. Examination of specimens from across the range of this species reveals substantial variation in shell color and size. The mantle margins in females are only slightly expanded into a modest flap. The flaps are light brown in coloration on the interior and freckled-brown on the exterior, and no eyespot is present. Short papillae are present along the margin of the flap, becoming larger anteriorly. In males, the mantle is only slightly expanded, without pigment, and with very short papillae. The marsupia are pisciform in shape, broader anteriorly and tapered behind, and darkly pigmented along the margin often with a darker spot of pigment anteriorly. The anus is unpigmented and the siphons are brownish. Glochidia were figured and described by O'Brien and Brim Box (1999).

Type Material: *Unio subangulatus* Lea, 1840, Lectotype USNM 85801 (Figures 9, 10) designated by Clench and Turner (1956). Type locality: Chattahoochee River, Columbus, [Muscogee Co.,] Georgia.
Unio kirklandianus S. H. Wright, 1897, Paratype USNM 149648. Type locality: Oclocknee River, Leon Co., Florida.

Remarks: *Hamiota subangulata* is listed as an endangered species (USFWS, 1998). The analysis of Roe et al. (2001) resolved this taxon as monophyletic and in a clade with *H. australis*.

Life History: Discharge of superconglutinate lures has been documented by O'Brien and Brim Box (1999) from late May through early June. *Micropterus punctulatus* and *M. salmoides* appear to be primary hosts for the species (O'Brien and Brim Box, 1999).

Range: *Hamiota subangulata* was found throughout the Apalachicola River Basin and the Ochlockonee River drainage (Brim Box and Williams, 2000). Currently the species continues to survive in some small streams and headwater rivers (USFWS, 1998).

Hamiota australis (Simpson, 1900) new combination

Lampsilis australis Simpson, 1900; Simpson, 1900a: 544; Simpson, 1900b: 75, pl. 2, fig. 2; Clench and Turner, 1956: 199, pl. 2, fig. 3.
Ligumia australis (Simpson, 1900); Haas, 1969: 432.
Villosa australis (Simpson, 1900); Heard, 1979: 44.

Description: Simpson (1900b) described the shells of this species as "long and elliptical . . . moderately inflated." The periostracum was described as "smooth, shinning, greenish yellow, rayed with green" and the nacre as "bright bluish white." Specimens examined were elliptical to elongate oval and often terminate in a blunt point. Specimens are almost always stained black, with some green rays visible on the posterior slope. The periostracum is often glossy. The right valve contains two pseudocardinal teeth, the smaller above the larger. The left valve has two compressed pseudocardinal teeth. Lateral teeth are elongate and slightly curved, two in the left valve and one in the right. Posterior mantle flaps are poorly developed with a streak of red stain along the margins. There is no eyespot on the mantle flap, and only a few very small papillae. The marsupia are pisciform, broadly rounded anteriorly and tapering behind (Figure 1). Color of the marsupium is white along the margin and black above. The anus is unpigmented and the incurrent and excurrent siphons are reddish in color. Glochidia were described and figured by Blalock-Herod et al. (2002).

Type Material: *Lampsilis australis* Simpson, 1900, Holotype USNM 150473 by original designation (Figures 5, 6). Type locality: Little Patsiliga Creek, southeastern Alabama.

Remarks: Fuller and Bereza (1973) stated that this species represented an "undescribed lampsiline genus" and that its marsupium allied it closely with *Ptychobranchus*. This species was incorrectly synonymized with *Ptychobranchus jonesi* (van der Schalie, 1934) by Clench and Turner (1956). The phylogenetic analysis of Roe et al. (2001) clearly placed this species with the other superconglutinate producers.

Life History: Superconglutinate releases have been documented in this species by Blalock-Herod et al. (2002). *Micropterus* spp. are likely hosts (Blalock-Herod et al., 2002).

Range: *Hamiota australis* was known historically from the Escambia, Yellow, and Choctawhatchee River systems. It continues to survive in some river and stream segments within these systems. This species is not currently protected under the Endangered Species Act.

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APPENDIX 1

SPECIMENS EXAMINED

Hamiota altilis

Alabama

Alabama River: USNM 25948; Alabama River, near Claiborne: ANSP 56419 [Lectotype *U. altilis* Conrad, 1834], ANSP 56418; Big Swamp Creek, Macon Co.: USNM 361723; Jackson Shoals, Choccolocco Creek: ANSP 103834, ANSP 103871; Beaver Creek: ANSP 103863; Coosa River: ANSP 41120, DMNH 130623; Coosa River, Coosa Valley: ANSP 103771; Higgin's Ferry, Coosa River, Chilton Co.: USNM 218118; McGowen's Ferry, near Wilsonville, Coosa River: USNM 521359; Weduska Shoals, Coosa River: ANSP 48001, DMNH 075252, DMNH 150037, DMNH 150038, USNM 348970, USNM 452169; Coosa River, [incomprehensible handwriting] Shoals, Shelby Co.: ANSP 341399; Shoal Creek, Pine Glen Recreational Area, Cleburne Co.: MMNS 7743, MMNS 8084, MMNS 8085, UAUC 120, UAUC 121, UAUC 125; Yellowleaf Creek, Jumbo, Chilton Co.: ANSP 89031; Cane Creek, West of CR 65, 2 mi. West CR 78 Jct., T15S, R11E, sec 3: UAUC 3292, MMNS 8081; Little Cane Creek, at CR 78, East of Edwardsville: UAUC 3293; Chewacla Creek at CR 22, ~4 mi. East of Tuskeegee, Macon Co.: UAUC 246, UAUC 247, UAUC 248; Uphappee Creek, 0.5 mi. upstream of Hwy. 29, Macon Co.: MMNS 8082; Cahaba River: USNM 152026; Cahaba River: ANSP 126054; Little Cahaba River, 0.5 mi. below Cahaba Beach Rd. bridge, Jefferson Co.: UAUC 149; Coosa River, Weduska Shoals, Shelby Co.: UF 3255; Coosa River at Fort William Shoals, Talladega Co.: UF 65420; Hurricane Creek, Cherokee Co.: UF 175098; Chewacla Creek, 8 mi. ESE of Tuskeegee Co. Rd. 22, Macon Co.: UF 202249; Shoal Creek, St. Clair Co.: UF 245989; Tuskeegee National Forest, Macon Co.: UF 266048; Cahaba River: UF 269576; Shoal Creek, St. Clair Co.: MMNS 8083.

Georgia

Etowah River: USNM 84936 [Lectotype, *U. doliaris* Lea, 1865]; Chattooga River: ANSP 89102; Chattooga

River, Chattooga Co.: USNM 59527; Chattanooga: USNM 25711 [Holotype, *U. gerhardtii*, Lea, 1862]; Fish Creek at Highway 278/ GA State Rt. 6, ~3.9 air mi. West of Rockmart, Polk Co.: UAUC 538, UAUC 539; Conasauga River at Tibbs Bridge Murray CR 109 (Whitfield CR100), Murray/Whitfield Co's.: UAUC 515, MMNS 8092; Conasauga River, Muskrat Midden, Tritogonia Shoals (CRM 46.70), Whitfield/Murray Co's.: UAUC 376; Conasauga River, south of state line, Murray Co.: MMNS 8090; Conasauga River: DMNH 150124, USNM 84937, USNM 348969; Etowah River: USNM 123202.

Tennessee

Conasauga River: DMNH 014683; Conasauga River, Conasauga: ANSP 341305, ANSP 347949; Conasauga River, Polk Co.: MMNS 8091.

Hamiota perovalis

Alabama

Alabama River: ANSP 56416 [Lectotype *U. perovalis* Conrad, 1834], ANSP 333496; Alabama River, Claiborne: USNM 84938; Coosa River: ANSP 56415; Coosa River, Gadsen: ANSP 126051; Coosa River, Talladega Co.: ANSP 126048; Black Warrior River: ANSP 88483; Mulberry River [Fork, Black Warrior River]: ANSP 88485; Rush Creek [Black Warrior River Dr.], FS Rt. 245, Winston Co.: MMNS 7745, MMNS 8088, UAUC 426; Flannigan Creek at FS Rd. 229, Lawrence Co.: MMNS 7744, UAUC 423, UAUC 424, UAUC 425; Toadvine, Valley Creek, Black Warrior River Dr., Jefferson Co.: UF 65302, UF 65304; Forks of the Warrior River, Walker Co.: UF 65305; North River, near Hagler's Mill, Black Warrior Dr., Tuscaloosa Co.: UF 65306; Sipsey Fork at N.F. 234, Bankhead National Forest, Winston Co.: UF 79069, UF 79072, UF 79082, UF 79085, UF 79136, UF 79137; Brushy Creek above Brushy Lake Recreational Area, Bankhead National Forest, Winston Co.: UF 79094; Capsey Creek, 50 mi. from Jct. with Brushy Creek, Bankhead N.F., Winston Co.: UF 79115; Sipsey Fork at mouth of Hurricane Creek, Bankhead National Forest, Winston Co.: UAUC 95; Brown Creek, Bankhead National Forest, Winston Co.: UAUC 1774; Alabama: ANSP 126049; North River, near Samantha [Black Warrior River], Tuscaloosa Co.: UAUC 107; Buttahatchee River, Hamilton: ANSP 100657, DMNH 075231; Tuscaloosa Co. Alabama: DMNH 146496; Black Warrior River, Jefferson Co.: UF 269609; Squaw Shoals, Black Warrior River, Jefferson Co.: UF 65298, UF 65299, UF 65300, UF 65303, UF 65307, UF 65429, UF 269518; Garden City, Mulberry Fork: UF 69207, UF 244558; Banks of Brushy Creek, at N.F. Rd. 255, Bankhead N.F, Winston Co.: UF 69269, UF 79177, UF 79178, MMNS 7748, MMNS 8089; Sipsey Fork, 1 mile N. of AL Hwy. 33 crossing, Winston Co.: UF 69279; Brushy Creek at N.F. Rd., Bankhead N.F., Winston Co.: UF 79076; Sipsey River at Sipsey Recreational Area, Bankhead N.F., Winston Co.: UF 79089; Borden's Creek, 1 mi., upstream of from Jct. Sipsey Fork, Sipsey Wilderness, Bankhead National Forest, Winston Co.: UF 79092, UF 79181; Sipsey Fork at N.F. Rd., 234, Bankhead National Forest, Winston Co.: UF 79139; Limestone Creek, 6.3 mi WNW of Monroeville, Monroe Co.: UF 197636; Blackwater Creek upstream from Harris bridge, Walker Co.: UF 266369; Sipsey River, 1.6 mi N. of Pleasant Ridge, Greene Co.: UF 197671; North River at Co. Hwy. 30, Fayette Co.: UF 197686; Sipsey River, 200 m. below Co. Hwy 23, Greene Co.: UF 197552; Sipsey River, 4–6 mi. below Co. Hwy. 2, Greene Co.: UF 197566; Sipsey River at CR 2, downstream of boat ramp, Pickens Co.: UAUC 156; Tombigbee River: ANSP 126053; Elrod, Sipsey River, Tombigbee R.: DMNH 146493; Lubbub Creek, at CR 24, 3.25 mi. Northeast of Aliceville, Pickens Co.: UAUC 67; Tombigbee River: USNM 159989; Lubbub Creek, 1.8 mi SSE of Aliceville above Hwy 14: UF 197619, UF 197632; Sipsey River, 3.6 mi. W. of Jena downstream of CR 2, Greene Co.: UF 197697; Sipsey River near confluence with Carpenter's Creek, Greene Co.: UF 197801; Sipsey River, 5.7 mi. NNE of Mantua, Greene Co.: UF 197857, UF 197862; Sipsey River, near Elrod, Tuscaloosa Co.: UF 269559, UF 65301; Trussels Creek at CR 19 bridge, Greene Co.: MMNS 8087.

Mississippi

Luxpalila Creek, near Columbus: USNM 84925 [Lectotype, *U. spillmanii* Lea, 1861], USNM 123279; Columbus, Lowndes Co.: UF 269560.

Hamiota subangulata

Alabama

Uchee Creek, Russell Co.: UAUC 116.

Florida

Chipola River, Look-Tremble Falls near Alpha, Calhoun Co.: ANSP 175750; Chipola River, near Pole Bluff landing, Calhoun Co.: ANSP 175751; Chipola River: ANSP 84324; Ochlockonee River: DMNH 150098; Ochlockonee River, Leon Co.: USNM 149648 [Paratype, *U. kirklandianus* S. H. Wright, 1897]; Ochlockonee River, Tallahassee, Leon Co.: ANSP 156892, ANSP 341307; Ochlockonee River, 7 mi. west of Tallahassee: ANSP 157553; Ochlockonee River, 10 mi. west of Tallahassee, Leon Co.: ANSP 159126; Ochlockonee River, 11 mi. northwest of Tallahassee: DMNH 119506; Ochlockonee River, 2 mi. west of Bloxham, Liberty Co.: ANSP 360553; Spring Creek, Marianna: ANSP 160210; State Rt. 167, 1 mi. north of Marianna, Chipola River, Jackson Co.: ANSP 349631; Spring Creek, Reynoldsville, Seminole Co.: UF 177; 1 mi. north Marianna, Chipola River: UF 390; 3.5 mi. east of Quincy, Little River: UF 415; ca. 2

mi. east of Clarksville, Chipola River, Calhoun Co.: UF 418; Chipola River, 9.2 km ENE Kinard, 12.5 km NW Lewis, 16.4 km N. Ida, Calhoun Co.: MMNS 8099.

Georgia

Chattahoochie River: ANSP 56477; Chattahoochie River, Columbus: USNM 85081 [Lectotype, *U. subangulatus* Lea, 1840]; ANSP 126272; Cooleewahee Creek, 0.9 mi. NE of Newton, Baker Co.: USNM 853746; Cooleewahee Creek at GA Rt. 91, Baker Co.: MMNS 8095; Abram's Inlet, Flint River: ANSP 190294; Mill Creek, Flint River, several mi. north of Albany: ANSP 267572; Kinchafoonee Creek at GA Rt. 41 crossing, just south of Preston, Webster Co.: UAUC591; Kinchafoonee Creek at GA Rt. 49 bridge ~9 air mi. northeast of Dawson, Terrell/Sumter Co's.: UAUC 602, UAUC 603, UAUC 604; Kinchafoonee Creek at GA Rt. 32, Lee Co., GA: MMNS 8096; Chickasawhatchee Creek at CR 130 bridge ~4 air mi. SW of Chickasawhatchee, Terrell Co.: UAUC 1753; Muckalee Creek at GA Rt. 195 bridge ~3.5 air mi. Northeast of Leesburg, Lee Co.: UAUC 312; Whitewater Creek on Morgan Mill Rd., Fayette Co.: UAUC 645; Ochlockonee River: DMNH 173390; Ochlockonee River, 7 mi. S. of Cairo: ANSP 194640, DMNH 048538, UF 412; Mimsville: ANSP 47892, DMNH 075151; Georgia: ANSP 126273; Calvary: ANSP 47891; Ochlockonee River, Thomas/Grady Co's. Georgia: MMNS 8101; Spring Creek at GA Rt. 84, Decatur Co.: MMNS 8094, MMNS 8100; Line Creek at GA Rt. 85/74 bridge, Coweta/Fayette Co.: MMNS 8097; Ichawaynochaway Creek at GA Rt. 216, Baker Co.: MMNS 8098.

Hamiota australis

Alabama

Andrews fish trap, Pea River, Barbour Co.: UF 65309; 7 mi. east of Brundidge, Pea River, Pike Co.: UF 123284; Bozemans landing, Conecuh River, near Crenshaw Co. line, Covington Co.: UF 65313; Lightwood Knot Creek, 1.6 mi. west of Opp, Covington Co.: ANSP#; Little Patsaliga Creek: USNM 150473 [Holotype, *Lampsilis australis,* Simpson, 1900]; West Fork Choctawhatchee River at Blue Spring State Park, Barbour Co.: UAUC 134, UAUC 511, UAUC 512, UAUC 513, UAUC 514; Little Choctawhatchie Creek, near Drian bridge, Houston Co.: UF 229532; Conecuh River on CR 28 ~1 mi. east of Goshen, Pike Co.: UAUC 510; Flat Creek at AL Hwy 153, near Flat Creek Church, Geneva Co.: UAUC 547; Five Runs Creek, Conecuh N. F., Covington Co.: MMNS 8086.

Florida

Shoal River at Hwy 85, 1 mi. south of I-10 Jct. in Crestview, Okaloosa Co.: UAUC 550, UAUC 551, UAUC 552, UAUC 643, UAUC 644; Shoal Creek, ca. 1 mi. above U. S. Highway 90, Okaloosa Co.: UF 261852; Limestone Creek, Walton: MMNS 7746, MMNS 7747.

Consideration of genetic relationships in management decisions for the endangered Anthony's riversnail, *Leptoxis crassa anthonyi* (Redfield, 1854) (Gastropoda: Pleuroceridae)

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ABSTRACT

Anthony's riversnail, *Leptoxis crassa anthonyi*, is a federally endangered pleurocerid restricted to three natural populations in the Tennessee River drainage. Recovery plans organized the three populations into two management units, and called for specific numbers of populations for downlisting or delisting. Given that nothing was known about the genetic structure of these populations and that individuals were being randomly transplanted, we examined each population using COI mtDNA sequences. All three populations possessed unique sequence haplotypes, and the two units identified in the recovery plan did not group the populations accurately in a phylogenetic context. Potential management decisions in light of our findings are discussed.

INTRODUCTION

Anthony's riversnail, *Leptoxis crassa anthonyi* (Redfield, 1854), is a pleurocerid gastropod currently listed as endangered by the United States Fish and Wildlife Service (USFWS) under the Endangered Species Act of 1973 as amended (USFWS, 1994). Adult shells of *L. crassa anthonyi* are large compared to sympatric pleurocerids, globose to ovate, greenish to greenish-brown in color, often with purple bands. The body whorl may be sculptured with low, indistinct tubercles, giving the shell a bumpy appearance. The aperture is ovate with a thin outer lip, and the columellar lip is reflected so that it covers a prominent umbilicus (Tryon, 1873). Historically, *L. crassa anthonyi* had been documented from the Tennessee River drainage in Alabama, Georgia and Tennessee, including the lower reaches of some of the larger tributaries (Burch and Tottenham, 1980; Bogan and Parmalee, 1983). Most populations of the species were extirpated when much of the Tennessee River and its tributaries were impounded by the Tennessee Valley Authority. Natural populations of *L. crassa anthonyi* persist at three localities: a small, scattered population in the main channel of the Tennessee River near the Alabama and Tennessee state line; a large population in Limestone Creek, Limestone County, Alabama; and a small population limited to a single stretch of the Sequatchie River, Marion County, Tennessee (Garner, 1994; Jenkinson, 1994; USFWS, 1997; Figure 1).

Two morphologically similar snails have occurred within the historic range of *Leptoxis crassa anthonyi*. The species often occurs sympatrically with *L. praerosa* (Say, 1821), and adults of *L. praerosa* are easily confused with juveniles of *L. crassa anthonyi* (Dillon and Ahlstedt, 1997). The other taxon, *L. crassa crassa* (Haldeman, 1841), was described as being similar to *L. crassa anthonyi* but with larger, more prominent tubercles on the body whorl, is presumed extinct (Turgeon et al., 1998). *Leptoxis crassa anthonyi* shells are most easily recognized as juveniles, given their saucer shape and the presence of a heavy carina that disappears with age (Dillon and Ahlstedt, 1997). The distinctness of *L. crassa anthonyi* has been supported by both allozyme (Dillon and Ahlstedt, 1997) and mitochondrial sequence data (Holznagel and Lydeard, 2000).

In 1997, USFWS published their recovery plan (USFWS, 1997) for *L. crassa anthonyi*. The plan identified two "populations" of *L. crassa anthonyi*: individuals from the Sequatchie and Tennessee Rivers as one population; and individuals from Limestone Creek as the other. Recovery criteria for *L. crassa anthonyi* were to protect the extant populations and to successfully re-establish other populations. If a total of four "populations" could be established, the species could be downlisted to threatened status; if six "populations" could be established, the species would be delisted entirely. Though the plan treated the three localities as two "populations," no effort had been made to determine if they were genetically homogeneous (i.e., a single genetic population) or genetically variable (i.e., two or three separate populations). In order to reach the stated goals of the recovery plan, the number of genetically distinct populations within the species needed to be determined. A working baseline of genetic information about each population was even more important due to reports of snails

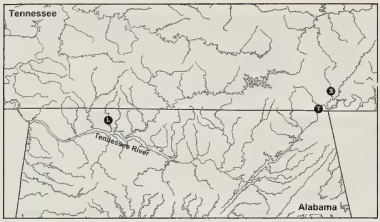

Figure 1. Map showing the locations of the three extant natural populations of *Leptoxis crassa anthonyi.* L = Limestone Creek; S = Sequatchie River; T = Tennessee River.

being translocated into existing populations and moved to new localities in the Tennessee River drainage (J. Garner and D. Hubbs, pers. comms.). In this study, we used mitochondrial DNA sequence data to conduct a comparative genetic analysis of extant *L. crassa anthonyi* populations to examine the degree of genetic differentiation among the three populations. Knowledge of the genetic structure would help direct management efforts in determining which populations could and should serve as sources for augmentations and reintroductions if desired.

MATERIALS AND METHODS

Adult specimens of *L. crassa anthonyi* from the three natural populations were collected under an endangered/threatened species subpermit (SA99-13). The maximum allowed number of specimens were collected, twenty from Limestone Creek, and five each from the Sequatchie and Tennessee Rivers (see Appendix 1). For comparative purposes, a reduced data set from previous analyses (Minton and Lydeard, 2003) was used to place *L. crassa anthonyi* in the proper systematic context. Fifteen individuals of *L. crassa anthonyi* from Limestone Creek and five each from the other two populations were included in the genetic study, along with four *L. praerosa,* each from different river drainages, and one each of the other taxa used in the previous study (Appendix 1).

Mitochondrial DNA sequences for a 1 kb portion of the cytochrome oxidase subunit I gene (COI) were generated using published methods (Minton and Lydeard, 2003) for genomic isolation, PCR amplification, and genetic analysis that followed. Sequences were aligned by eye (Hall, 1999) and phylogenetic hypotheses generated by PAUP° 4.0b10 (Swofford, 2002) under maximum parsimony with the following options: 50 replicates of heuristic search with random addition, uninformative characters were ignored, branches with minimum zero length collapsed, and minimal length trees kept. This gene fragment showed significant phylogenetic signal and no base composition bias or sequence saturation in a more inclusive pleurocerid dataset (Minton and Lydeard, 2003). Internal branch stability was assessed by jackknife (Farris et al., 1996) and Bremer support (Bremer, 1994).

RESULTS

Aligned sequences resulted in a data matrix of 890 characters, of which 222 were parsimony-informative. Each population of *Leptoxis crassa anthonyi* possessed a unique haplotype, and all individuals from a population shared the same haplotype. Maximum parsimony analysis yielded two trees (Figure 2, strict consensus). All specimens of *L. crassa anthonyi* constituted a monophyletic group. Uncorrected p-distances were 1.46% between the Limestone Creek and Sequatchie River spec-

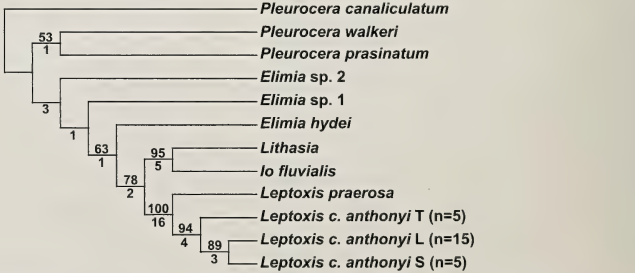

Figure 2. Strict consensus of two most parsimonious trees (TL = 718, CI = 0.54) based on mitochondrial COI sequences. *Leptoxis crassa anthonyi* specimens identified as in Figure 1. Jackknife values >50% above branches, Bremer values below. Composition of *Leptoxis* and *Lithasia* clades are given in Table 1; both clades were monophyletic with jackknife support >50% and Bremer support >1.

imens, 2.02% between the Limestone Creek and Tennessee River specimens, and 3.03% between the Sequatchie and Tennessee River specimens. The *L. crassa anthonyi* clade was sister to a clade of *L. praerosa* specimens. Most clades were well supported by jackknife and Bremer values, as were the relationships within each clade.

DISCUSSION

Our results further support the validity of *Leptoxis crassa anthonyi* and its distinctiveness from *L. praerosa*, and show each of the three populations of *L. crassa anthonyi* to be genetically unique based on COI haplotypes. Uncorrected pairwise genetic differences between the three populations of *L. crassa anthonyi* were consistent with published intraspecific differences seen in other pleurocerids using COI sequences (Minton and Lydeard, 2003). The USFWS recovery plan calls for the presence of no fewer than four viable populations of *L. crassa anthonyi* before any change in listing status can occur. For establishment of new populations, introductions of each haplotype to new areas within their current river system would be preferred in order to avoid mixing of unique evolutionary entities and possible elimination of the current genetic diversity.

The USFWS has designated *Leptoxis crassa anthonyi* from the Sequatchie and Tennessee Rviers as a single population. Based on that assumption, their management efforts might target one of the populations as a source for augmenting the other. If translocations are to be used, our analysis suggests that the Limestone Creek population would be a better option for augmenting the Sequatchie River population due to lower genetic difference. Additionally, if a single population is to serve as a source of new introductions and augmentations, recent survey work (J. Garner, pers. comm.) indicates that Limestone Creek would be preferred because of its large population size. Regardless, controlled experimental populations should be established, either in the field or laboratory, that could be monitored genetically and for population growth and be compared with non-augmented populations to determine whether fitness has been enhanced or diminished from the introduction of unique haplotypes from other populations. This measure would be especially prudent given that haplotypes are being randomly introduced through human activity. Any recovery plan that involves translocation of *L. crassa anthonyi* should use juveniles, as they are more easily identified by their strong keel. This will help ensure the movement of *L. crassa anthonyi* and potentially prevent the introduction of adult, non-endemic *L. praerosa.*

ACKNOWLEDGMENTS

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Appendix 1. Systematic list of taxa and specimens used in this study. Complete locality information is available from the authors. UAG = University of Alabama gastropod collection.

Taxon	Locality	UAG voucher	Genbank accession
Genus *Elimia*			
E. hydei	Black Warrior River, Tuscaloosa Co., AL	UAG 584	AF435775
Elimia sp. 1	Green River, Hart Co., KY	UAG 574	AF435759
Elimia sp. 2	Collins River, Warren Co., TN	UAG 407	AF435761
Genus *Io*			
Io fluvialis	Clinch River, Hancock Co., TN	UAG 585	AF435776
Genus *Leptoxis*			
L. crassa anthonyi	Limestone Creek, Limestone Co., AL	UAG 581	AF435772
	Sequatchie River, Marion Co., TN	UAG 582	AF435773
	Tennessee River, Jackson Co., AL	UAG 583	AF435774
L. praerosa	Harpeth River, Davidson Co., TN	UAG 404	AF435779
	Shoal Creek, Lawrence Co., AL	UAG 560	AF435780
	Sequatchie River, Marion Co., TN	UAG 588	AF435781
	Tennessee River, Jackson Co., AL	UAG 589	AF435782
Genus *Lithasia*			
L. armigera	Harpeth River, Cheatham Co., TN	UAG 555	AF435739
L. geniculata fuliginosa	Red River, Robertson Co., TN	UAG 398	AF435754
	Duck River, Maury Co., TN	UAG 403	AF435749
	Buffolo River, Humphreys Co., TN	UAG 406	AF435747
L. lima	Bear Creek, Colbert Co., AL	UAG 570	AF435757
L. verrucosa	French Broad River, Knox Co., TN	UAG 576	AF435767
	White River, Woodruff Co., AR	UAG 577	AF435771
Genus *Pleurocera*			
P. canaliculatum	Duck River, Maury Co., TN	UAG 590	AF435783
P. prasinatum	Yellowleaf Creek, Shelby Co., AL	UAG 591	AF435784
P. walkeri	Shoal Creek, Lauderdale Co., AL	UAG 592	AF435785

Fallen into oblivion—the systematic affinities of the enigmatic *Sulcospira* Troschel, 1858 (Cerithioidea: Pachychilidae), a genus of viviparous freshwater gastropods from Java

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ABSTRACT

Sulcospira Troschel, 1858, is not only the taxonomically oldest but also one of the most poorly known genera of Southeast Asian Pachychilidae. It serves as an instructive case study as to how the puzzling systematics of freshwater Cerithioidea has hampered a deeper understanding of their phylogeny and evolution. The genus has been established for the Javan freshwater gastropod *Melania sulcospira* Mousson, 1849, on the grounds of its round, multispiral operculum and an elongated main cusp in the central radula teeth. Although of great systematic significance, this taxon has been widely ignored by subsequent authors. We here recapitulate the taxonomic history of the genus and describe and evaluate the morphological properties of the type species *S. sulcospira* on basis of the limited existing material, in order to facilitate a better understanding of pachychilid systematics. In addition, in an attempt to clarify its systematic affinity, we compare the properties of another allegedly related species from Java, *S. martini* (Schepmann, 1898). We show that these two viviparous species exhibit different protoconch morphologies, which are indicative of reproductive strategies distinct from other pachychilids. Finally, we outline preliminary suggestions as to the systematics of *Sulcospira* within the family Pachychilidae.

MATERIALS AND METHODS

Materials

This study is based on the examination of material from various museum collections worldwide (see repositories). All of these samples comprise dry shells only, which as a rule were empty. Only few shells contained fragmentary soft parts; some of them were re-hydrated for examinations. However, these bodies generally did not facilitate morphological examinations except for the extraction of small radula fragments. We have not tried to extract DNA from dried tissues because earlier attempts with comparable material of *Brotia* failed. In order to acquire fresh material, collecting trips have been undertaken in 2000 and 2002. We have searched rivers and creeks in different sectors of there course (i.e. upstream, midstream, downstream) for a period of altogether 7 days in West Java (along the roads between Jakarta and Serang, Bogor and Sukabumi, Sukabumi and Pelabuhan Ratu, Bogor and Cipanas, Bogor and Cianjur, in the Botanical Garden Bogor) and for 3 days in East Java (between Taksimalaya, Cipatujah, and Pangadaran). During these trips we were not able to find any material of *Sulcospira*, though.

Because freshwater biotopes on Java are facing dramatic devastation by a multitude of causes related to the dense population on this island such as pollution, flow regulation, drainage, impoundment and a general degradation of collecting areas by agriculture, industry and settlements (own observations; see also Dudgeon, 2000, for SE Asia in general), we believe that *S. sulcospira* has become extinct in vast areas on Java. It remains unclear whether and at which localities populations of this species still exist.

Repository Institutions

Voucher material is housed with the following museums: Natural History Museum, London (BMNH), Museum of Comparative Zoology, Cambridge, Mass. (MCZ), Muséum d'Histoire Naturelle, Genève (MHNG), Muséum National d'Histoire Naturelle, Paris (MNHN), Natural History Museum Naturalis, Leiden (RMNH), Senckenbergmuseum, Frankfurt/Main (SMF), Zoölogisch Museum, Amsterdam (ZMA), Museum für Naturkunde, Berlin (ZMB).

We were not able to locate material in the following museum collections: Academy of Natural Sciences, Phil-

adelphia (ANSP), United States National Museum, Washington (UNSM), Zoologisches Institut und Museum, Universität Hamburg (ZMH), Zoologische Staatssammlung, München (ZSM).

Morphological Examinations

Dimensions of all shells were measured to 0.1 mm precision. The shell height (H) is the maximum dimension parallel to the axis of coiling, breadth (B) the maximum dimension perpendicular to H, including the aperture. The length of the aperture (LA) is the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip, the width (WA) the greatest length perpendicular to LA. The height of the body whorl (BW) is the distance from the base of the shell to the upper suture of the first whorl exactly above the junction of the outer lip with the penultimate whorl. Morphometrical parameters used in the analyses, beside the shell dimensions, were: H/B, H/LA, H/BW, H/LA and B/BW. These shell parameters were statistically analyzed by performing t-tests, one-way ANOVA, and a discriminate analysis.

Protoconchs removed from dried adults were cleaned by soaking in 10% KOH solution, flushed in distilled water, and sonicated to remove residual contaminations prior to scanning electron microscopy. Radulae were taken from dried shells or from historic preparations. Radulae from dried shells were enzymatically cleaned as described by Holznagel (1998); an old radula embedded in Canada balsam was cleaned with xylene followed by sonication. Radulae and juvenile shells were mounted on aluminum specimen stubs using adhesive carbon tabs or double-sided tape, respectively, and coated with gold-palladium for 120 s at 20 mA for examination under a scanning electron microscope (LEO 1450 VP) at 10 keV.

Nomenclatorial Remarks

Some species-group names introduced by Troschel (1857–1858) are open to discussion. Bouchet (pers. comm.) argued that the usage of the names Bithyniae, Lithoglyphi, Hydrobiae, Ancyloti, Thiarae, and Pachychili by Troschel (op. cit.) contrasts with the rest of his work (Troschel, 1856–1863), in which he stated the ranks of the categories he used and formed names with endings -idea, -ina, or -acea. Because Troschel stated explicitly that he refrained from allocating these groupings at family rank given the somewhat ambiguous morphological data he was faced with, it was suggested that one should ignore these names (Bouchet, pers. comm.). However, some of these names, such as Bithyniidae, Thiaridae, or Hydrobiidae, have been usually published with Troschel (1857–1858) as author. Unless otherwise stipulated, we prefer to refer to Troschel (1857–1858) as author of these names not only because we regard them as available and valid but also in order to maintain stability in their usage; for a statement to the contrary see Bouchet and Rocroi (submitted).

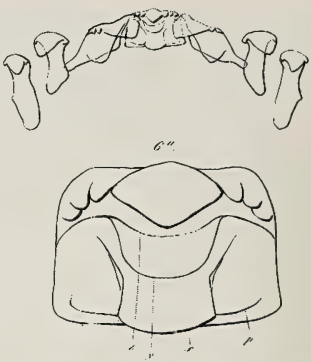


Figure 1. Original drawing of the radula of "*Sulcospira typica* (*Melania sulcospira* Mousson)" by Troschel (1858: pl. 9, fig. 6). In the upper part of the figure a row of teeth is shown comprising a rachidian flanked on each side by a lateral tooth and an inner and outer marginal tooth; a magnified representation of the rachidian is shown below. Characteristics that are typical for Pachychilidae are, e.g., the enlarged main cusp of the rachidian and lateral teeth, respectively, which is flanked by three (or two) smaller cusps on each side that taper in size; the presence and shape of the glabella (or ramp); and marginal teeth possessing two cusps.

Nomenclatorial aspects raised in this paper refer to the stipulations of the 4th edition of the International Code of Zoological Nomenclature ("ICZN") issued by the International Commission of Zoological Nomenclature (1999).

RESULTS

Sulcospira Troschel, 1858

Sulcospira Troschel, 1858: 117–118; Brot, 1874: 56; Thiele, 1929: 190; Morrison, 1954: 381.

Diagnosis: *Sulcospira* possesses a rather conical shell sculptured by spiral lirae; axial sculptural elements are lacking. Protoconchs possess a smooth sculpture with a fine granular texture or faint growth lines.

Type Species: *Melania sulcospira* Mousson, 1849, by monotypy.

Nomenclature and Systematics: The genus *Sulcospira* was described by Troschel (1858) for the Javan species *M. sulcospira* exhibiting certain characteristics that were held to be peculiar of this species, namely a round, multispiral operculum with four regular whorls and the radula with an enlarged main cusp of the rachidian (Figure 1, 17–18). Troschel (1858: 114) based his description on material received from August Brot in Genève, i.e.,

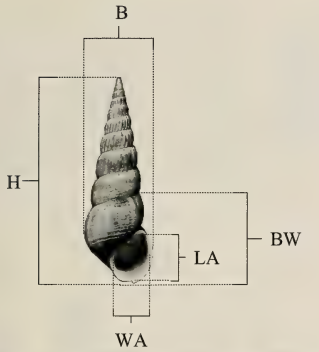


Figure 2. Shell dimensions. B: breadth; BW: weight of the body whorl; H: height; LA: length of the aperture; WA: width of the aperture.

on material that is likely housed at MHNG today (see Material Examined).

Sulcospira represents the oldest available generic name established for representatives of the Southeast Asian Pachychilidae and is here considered valid. However, the diagnosis of Troschel (1858) is not sufficient to characterize the taxon unambiguously. Neither a round and multispiral operculum with four whorls nor the possession of a pronounced main cusp of the rachidian are considered as diagnostic features of *Sulcospira* alone (see discussion). Nonetheless, these features characterize *Sulcospira* as a member of the Pachychilidae (Glaubrecht, 1996, 1999; Köhler and Glaubrecht, 2001, 2002, 2003).

In more recent literature *Sulcospira* has been widely ignored. Thiele (1929) suggested subdividing *Sulcospira* into two subgenera, *Sulcospira* and *Tylomelania* F. and P. Sarasin, 1898. According to Thiele, *Sulcospira* would include *Paracrostoma, Acrostoma* Brot, 1870, and *Brotella* Rovereto, 1899, as junior synonyms, consequently comprising two species: *S. sulcospira* from Java and *S. huegeli* (Philippi, 1843) from South India. *Tylomelania,* however, was considered to encompass a small number of species restricted to Sulawesi.

This concept of Thiele (1929) led Subba Rao (1989: 107) to wrongly assume that *M. huegeli* would be the type species of *Sulcospira,* which it is not (see Troschel's original designation).

Later authors had different taxonomic views. Morrison (1954) followed Abbott (1948) but not Thiele (1929) and treated *Acrostoma, Brotella,* and *Paracrostoma* as synonyms of *Brotia,* while considering *Tylomelania* as a genus on its own. He also claimed that our understanding of *Sulcospira* is not satisfactory. Based on some superficial similarities with *Brotia,* but also with *Tylomelania* and *Balanocochlis* (a thiarid), Morrison (1954) proposed the allocation of *Sulcospira* "tentatively to the *Melanoides* complex". Since *Melanoides* is a thiarid, this allocation is rejected here.

All these classification schemes were suggested in absence of phylogenetic analyses of morphological characters. In addition to the type species, other taxa have been assigned to the genus by previous authors, although this has not been done consistently (Table 1). The various opinions led also to different assumptions on the species circumscription and diversity of this taxon. For example, Brot (1874) subsumed a number of taxa under *Sulcospira,* of which we currently only consider two to be actually pachychilids: *Melania spadicea* Reeve, 1860, and *M. hainanensis* Brot, 1872. Yen (1939) added two more taxa, *M. ebenina* Brot, 1883, and *M. biconica* Brot, 1886. Boettger (1890), Oostingh (1932), and Adam and Leloup (1838) treated *M. testudinaria* von dem Busch, 1842, as member of *Sulcospira* but did not mention the former taxa. In contrast, other authors assigned those taxa to *Brotia* instead (Rensch, 1934; Benthem-Jutting, 1956, 1959; Knipper, 1958; Dudgeon, 1982, 1989; Köhler and Glaubrecht, 2001, 2002). Eventually, Benthem-Jutting (1956) assumed that *S. sulcospira* is the only representative of the genus.

In order to clarify the puzzling taxonomy and systematics, a revision of *Sulcospira* with an evaluation of its anatomical characters is needed. A sound classification has to be based on autapomorphic features, which is lacking to date. Unfortunately, a comprehensive description of the morphology of *Sulcospira* suffers from the

Table 1. Comparison of previous views on the systematics and circumscription of *Sulcospira.*

	Authors			
	Brot (1874)	Thiele (1929)	Morrison (1954); Benthem-Jutting (1956)	Köhler and Glaubrecht (2002)
Taxonomy at generic level	*Melania* (*Sulcospira*)	*Sulcospira* (*Sulcospira*), *Sulcospira* (*Tylomelania*)	*Sulcospira*	*Sulcospira*
Included taxa	*M. sulcospira, M. spadicea, M. hainanensis,* and other non-pachychilid taxa	*S. sulcospira, S. huegeli, T. neritiformis, T. carbo, T. porcellanica*	*S. sulcospira*	*S. sulcospira, S. spadicea*

Table 2. Shell parameters [mm] of *S. sulcospira* and *S. martini*. Abbreviations: B: breadth; BW: weight of the body whorl; H: height; LA: length of the aperture; m: median; N: number of whorls; No: number of shells; sd: standard deviation; WA: width of the aperture.

Lot		No	H	B	LA	WA	BW	N
***S. sulcospira* (total)**	**m**	**26**	**19.3**	**10.1**	**9.5**	**4.9**	**14.3**	**4.7**
	sd		**2.5**	**1.3**	**1.0**	**0.6**	**1.9**	**0.5**
Holotype *M. sulcospira*		1	23.2	12.0	9.7	5.0	15.2	4.0
S. sulcospira (ZMA)	m	21	19.5	10.2	9.5	4.9	14.4	4.6
	sd		2.2	1.2	0.9	0.5	0.6	0.6
S. sulcospira (MNHN)	m	4	18.7	9.9	9.3	4.9	14.1	4.8
	sd		3.6	1.8	1.5	0.9	2.9	0.4
***S. martini* (total)**	**m**	**58**	**27.6**	**12.0**	**11.0**	**5.9**	**17.7**	**6.0**
	sd		**4.5**	**1.5**	**1.3**	**0.8**	**2.1**	**1.0**
Syntypes *M. spadicea* (BMNH 19990497)	m	3	25.5	11.6	10.2	5.2	16.1	6.0
	sd		0.7	0.2	0.9	0.6	0.9	0.5
Syntypes *M. junghuhni* (RMNH, ZMA)	m	22	29.9	12.4	11.6	6.0	18.4	6.3
	sd		4.6	1.8	1.4	0.9	2.4	0.7
Syntypes var. *flamnulata*, var. *fasciata* (RMNH)	m	16	28.7	12.3	11.7	6.1	17.9	6.6
	sd		2.9	1.2	1.1	0.7	1.7	0.6
S. martini (ZMB 4.074)	m	17	23.8	11.2	11.0	5.7	16.9	4.9
	sd		2.9	1.3	1.0	0.5	1.7	0.7

lack of well-preserved material of the type species. We compile below the anatomical data based on the material of *S. sulcospira* available.

Sulcospira sulcospira (Mousson, 1849)

Melania sulcospira Mousson, 1849a [1848]: 269; Mousson, 1849b; 68, pl. 9, fig. 3; Martens, 1897: 245 (*partim*); Leschke, 1914: 251.

Sulcospira typica Troschel, 1858: 117, 118, pl. 9, fig. 6 [introduced as replacement name for *M. sulcospira* Mousson, 1849].

Pachycheilus sulcospira [sic].—H. and A. Adams, 1858: 299.

Melania (*Sulcospira*) *sulcospira*.—Brot, 1870: 277; Brot, 1874: 56–57, pl. 6, fig. 11; Boettger, 1890: 245.

Sulcospira sulcospira.—Morrison, 1954: 381; Köhler and Glaubrecht, 2002: 149, fig. 3 L.

Diagnosis: Shell relatively small (Table 2), conical with spiral lirae, and a subsutural depression; aperture elongately ovate, abapically flared. Radula with squarish rachidian exhibiting a straight upper and lower rim, the cutting edge of all teeth with one very pronounced main cusp of triangular shape.

Description: *Shell* (Figures 3–5): small, ovate to conical, solid, spire with eroded apex and up to six flattened whorls, separated by a narrow suture; sculpture consisting of fine, regular spiral lirae that are most prominent at the base and may almost lack on upper whorls, and faint growth lines; whorls with a subsutural depression; color from yellowish to olive or dark brown. Aperture elongately ovate, abapically flared, peristome sharp; columella slightly bent and thickened.

Protoconch (Figures 19–20): Relatively large, compared to the adult; with height of about 1.2 mm comprising one and a half whorl; generally smooth. Apical whorl inflated, dome-shaped, with a granular surface sculpture, transition in sculpture visible on first whorl from granular to faint growth lines. One sample of four specimens housed at MNHN (ex coll. Staat) has a label stating that "about 140 embryos were obtained from the large specimen". However, the fate of these protoconchs is unknown.

Operculum: With four whorls regularly increasing in diameter and a sub-central nucleus.

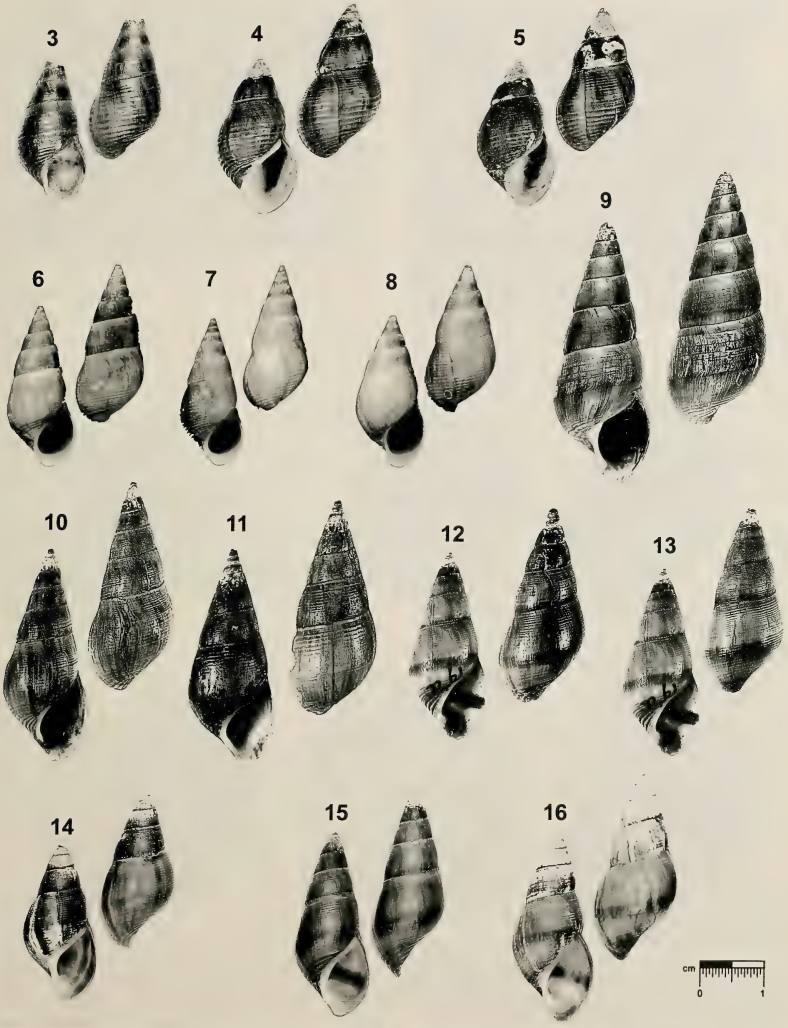
Radula (Figures 16–17): Rachidian tooth squarish with a straight upper and lower rim, cutting edge with one heavily enlarged main cusp of triangular shape, flanked by two, much smaller accessory cusps on each side; glabella well developed, rather rectangular with a rounded basal margin not exceeding the lower rim of the rachidian tooth, lateral margins straight and not well defined. Lateral teeth with one heavily enlarged main cusp, and considerably smaller accessory cusps, one at the outer side, two or three at the inner side. Inner and outer marginal teeth with two cusps, the outer one being very large, triangular in shape, and the inner one being pointed and small. Inner marginal teeth broader than outer marginals. Outer lateral flange inconspicuous.

Anatomy: Unknown.

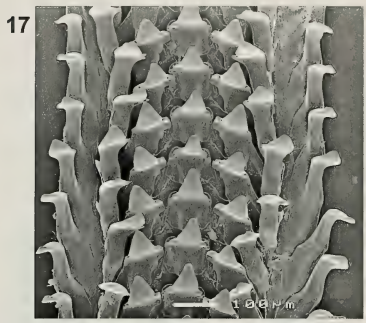
Type Material: Indonesia: Holotype ZMZ 522306, Indonesia: Java, leg. Zollinger (Figure 3) [Mousson, 1849b refers to "das einzige Exemplar dieser Art . . ." = the only specimen of this species . . .].

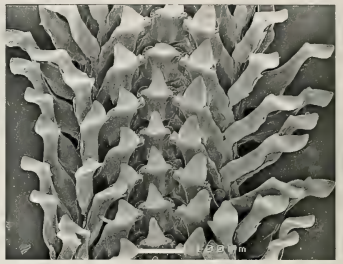
Type Locality: "Java", Indonesia.

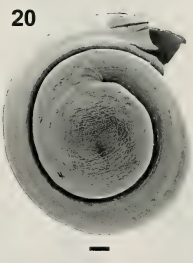
Other Material Examined: Indonesia: Java (MHNG; MNHN; MNHN, ex coll. Staat; ZMA (2 lots); ZMB 200.101) (if not stated otherwise, a single lot from each collection, mostly without reference number, was examined); museums without material: ANSP, BMNH, MCZ, RMNH, SMF, USNM, ZMH, ZSM.

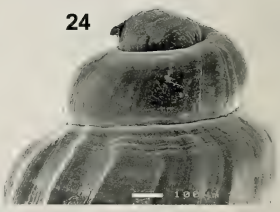


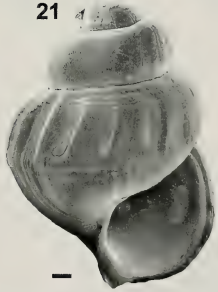
Figures 3–16. Shell morphology of *Sulcospira sulcospira* (**3–5**) and *S. martini* (**6–16**) (apertural and abapertural, respectively). **3.** *S. sulcospira*. Holotype (ZMZ 522306). **4–5.** *S. martini*. Two shells from Java (ZMA). **6.** Lectotype of *M. spadicea* (BMNH 19990497/A). **7–8.** Two paralectotypes of *M. spadicea* (BMNH 19990497/B). **9.** Lectotype of *M. junghuhni* (RMNH 71326). **10–11.** Two syntypes of *M. junghuhni* var. *flammulata* (RMNH 71327). **12–13.** Two syntypes of *M. junghuhni* var. *fasciata* (RMNH 71328). **14–16.** Three shells from Java, Malangbong (ZMB 4.074). Scale bar = 10 mm.











Figures 17–24. SEM images of the radula and juvenile shells removed from dry shells of *S. sulcospira* (**17–20**) and *S. martini* (**21–24**). *S. sulcospira*: **17.** Radula (ZMA). **18.** Radula (ZMB 200.101). **19.** Juvenile shell, apertural view (ZMA). *S. martini*: **20.** Juvenile shell, apical view (ZMA). **21.** Juvenile shell, apertural view (ZMA 4.074). **22–23.** Apical view. **24.** Detail of the apical portion. Scale bars = 100 μm.

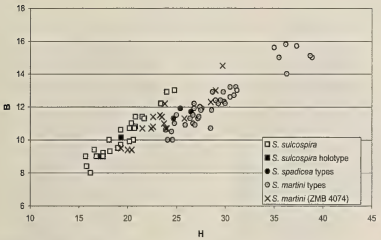


Figure 25. Comparison of the shells of *S. sulcospira* and *S. martini* based on shell parameters height (H) and breadth (B).

Distribution: Indonesia: Java. More precise localities were given by Boettger (1890: Bogor Botanical Garden) and Martens (1997: Jakarta, Malangbong, Cipanas). However, the material of Boettger could not be traced (SMF?), and Martens misidentified material of *Melanoides tuberculata* (Cipanas) and *S. martini* (Malangbong; ZMB 4.076); no voucher material was found from Jakarta.

Nomenclature and Systematics: *Melania sulcospira* is the type species of the genus *Sulcospira* by original designation. When describing the new genus, Troschel (1858), mentioned *M. sulcospira* as the "typical species", and introduced the name *S. typica* for the same taxon as a new, unnecessary substitute name meant to replace an older available name (*nomen novum*). Thus, *S. typica* is a junior synonym of *S. sulcospira* (ICZN Art. 72.7.). *Sulcospira typica* is invalidated as potential type name (ICZN Art. 68.4.) making *M. sulcospira* the type by absolute autonomy. Martens (1897) assumed that *M. spadicea* is a synonym of this species, which was rejected by Leschke (1914) and Benthem-Jutting (1956: 373), stating that Martens (1897) had misidentified specimens of *Melanoides tuberculata* for *M. spadicea.*

Remarks: Compared to *Sulcospira martini, S. sulcospira* is more conical in shape; the former lacks a conspicuous subsutural depression. Most conspicuously, both species differ in their protoconch morphology. Shells of *B. testudinaria* are more elongated in shape, attain a larger size (between 25 to 40 mm in shell height), lack a subsutural depression, and exhibit a different radular morphology: e.g., rachidian with inflated and rounded upper corners, a smaller main cusp, marginal teeth possess two equally shaped cusps.

Given the scarcity of material and imprecise earlier locality data for this material, we tried to restrict the type locality from historical accounts. The Swiss malacologist Albert Mousson (1805–1890) based his descriptions on material collected by the Swiss botanist Heinrich Zollinger (1818–1859), who traveled in Indonesia between 1842 and 1848. However, as Zollinger collected not only

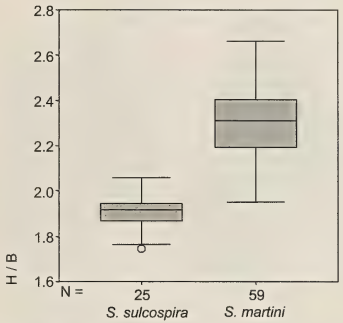


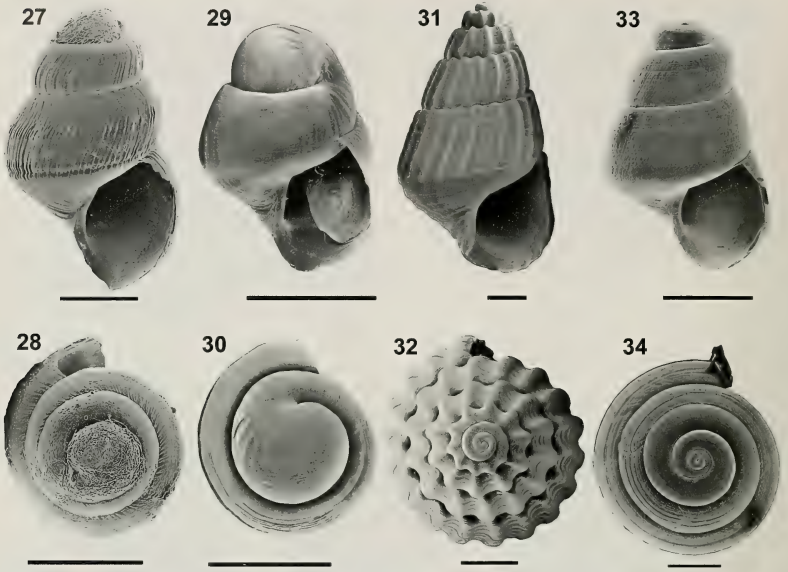
Figure 26. Comparison of *S. sulcospira* and *S. martini* based on shell parameters ratio H/B. Box plot diagram showing the median, the 25%- and 75%-percentile and largest non-extremes (less than 1.5 times of box height).

in West Java, but later also in East Java, and on some other islands (Wanner, 1984), it turned out that a restriction of the type locality is not possible and "Java" remains as the only known reference.

Sulcospira(?) *martini* (Schepmann, 1898)

Melania spadicea Reeve, 1860: pl. 19, species 132 (not *Melania spadicea* Philippi, 1849); Brot, 1870: 277.
Melania (*Sulcospira*) *spadicea.*—Brot, 1874: 57–58, pl. 6, fig. 12.
Brotia spadicea.—Benthem-Jutting, 1956: 372–373, fig. 75.
Sulcospira spadicea.—Köhler and Glaubrecht, 2002: 148, fig. 3G.
Melania junghuhni Schepman, 1896: 135–136, pl. 2, fig. 1. ("Java"; lectotype and 41 paralectotypes RMNH 71326; 24 paralectotypes ZMA; two paralectotypes SMF 292406; var. *flammulata*: 16 syntypes RMNH 71327; 3 syntypes MCZ 96926, var. *fasciata*: 18 syntypes RMNH 71328; 24 syntypes ZMA; 8 syntypes MCZ 96898) (not *M. junghuhni* Martin, 1879); Leschke, 1914: 251; Benthem-Jutting, 1929: 84.
Melania martini Schepmann, 1898: 84.
Brotia testudinaria.—Köhler and Glaubrecht, 2001: 301–304 (*partim*); Köhler and Glaubrecht, 2002: 140, 141, 150 (partim).

Diagnosis: Conical shell with convex to flattened whorls sculptured with fine spiral ridges. Protoconch with about 2.5 regular whorls; apical whorl not inflated, no transition in shell structure is visible in the first two whorls. Axial ribs may be present in the juvenile shell from the second whorl on. Most conspicuously distinguished from all other pachychilids by its protoconch morphology (Figures 27–34); distinguishable from *S. sulcospira* by its more elongated and larger shell (Figure 26); though adult shell not distinguishable from *B. testudinaria.*



Figures 27–34. Comparison of protoconchs of different southeastern Asian Pachychilidae (apertural and apical view, respectively). **27–28.** *Brotia costula.* **29–30.** *Brotia hainanensis.* **31–32.** *Tylomelania patriarchalis* (with kind permission of Thomas von Rintelen). **33–34.** *Pseudopotamis semoni.* Scale bars = 100 μm.

Description: *Shell* (Figures 6–16): Small to medium sized (Table 2), ovate to conical, spire with eroded apex and eight to ten flattened whorls; sculpture consisting of fine, closely spaced regular spiral lirae, may lack almost completely, and faint growth lines; color yellowish brown to olive, brown spiral band or patches may be present. Aperture elongated ovate, produced below, peristome sharp.

Protoconch (Figures 21–24): Height of about 1.2 mm comprising 2½ whorls; apical whorl not inflated, corresponding to the regular diameter of the subsequent whorls; first two whorls smooth, only faint growth lines visible, without transition in sculpture, from the second whorl on smooth axial ribs may be present.

Operculum: Consisting of three whorls and a sub-basal nucleus Brot (1874).

Anatomy and Radula: Unknown.

Type Material: Indonesia, Java: Lectotype and 41 paralectotypes of *M. junghuhni,* RMNH 71326, leg. Junghuhn (Figure 9), designated by Köhler and Glaubrecht (2002); 24 paralectotypes, ZMA; two paralectotypes, SMF 292406; 16 syntypes of *M. junghuhni* var. *flammulata,* RMNH 71327; three syntypes, MCZ 96926, 18 syntypes of *M. junghuhni* var. *fasciata,* RMNH 71328; eight syntypes, MCZ 96898. Without locality: Lectotype of *M. spadicea,* BMNH 19990497/A, Cuming collection, designated by Köhler and Glaubrecht (2002); two paralectotypes, BMNH 19990497/2.

Type Locality: "Java", Indonesia.

Other Material Examined: Without locality (ZMA; MHNG); Indonesia: Java (MHNG), Malangbon (ZMB 4.074) (a single lot from each collection, mostly without reference number). No material was found in the following museums: ANSP, MNHN, SMF, USNM, ZMH, ZSM.

Nomenclature and Systematics: *Melania spadicea* Reeve, 1860, is a primary homonym of *M. spadicea* Philippi, 1849 (ICZN Art. 53.3) and, as such, is permanently invalid (ICZN Art. 57.2). The next available names are *M. junghuhni* Schepmann, 1896, *M. junghuhni* var. *flam-*

mulata Schepmann, 1896, and *M. junghuhni* var. *fasciata* Schepmann, 1896. However, the first is a primary homonym of *Melania junghuhni* Martin, 1879, a fossil species from Java, as stated by Schepmann (1898). The other two are junior primary synonyms of *Melania flammulata* von dem Busch in Philippi, 1843, and *Melania fasciata* Menke, 1828, respectively.

Schepmann (1898) suggested *Melania martini* as a replacement name for *M. junghuhni,* which is the valid name for this taxon. The two color morphs described by Schepmann (1896), *fasciata* and *flammulata,* are not considered here to represent extant evolutionary entities and therefore are treated as junior synonyms of *M. martini.*

The classification of this species by former authors is inconsistent. Benthem-Jutting (1956) considered it to be a member of *Brotia*; but unaware of the fact that *M. spadicea* Reeve, 1860, is not valid she assumed that this name had priority over *M. martini.* Köhler and Glaubrecht (2002) assumed that *M. martini* and *M. spadicea* are distinct and treated the former as a synonym of *B. testudinaria* and the latter as a species closely related to *S. sulcospira* as was suggested earlier by Brot (1874).

Distribution: Java, as the only known locality. Malangbon in Central Java, east of Bandung, is the only known exact locality (ZMB 4.074, catalogued in 1859).

Analyses of Shell Morphometry: *Sulcospira martini* can be distinguished from *S. sulcospira* by its higher shell and more slender shape (see analyses of shell parameters below). However, to differentiate between shells of "*M. sulcospira*" and "*M. martini*" is no easy task; contradictory statements on their taxonomy abound in earlier accounts (Brot, 1874; Benthem-Jutting, 1956; Köhler and Glaubrecht, 2002). In fact, shells exhibit a very similar shape, sculpture, and coloration. However, the two taxa can be distinguished by statistical analyses of shell morphometry. We used one-way ANOVA and t-test for two independent groups of variables to discriminate specimens that were assigned beforehand either to *S. sulcospira* or to *S. martini* according to their shell morphology. The t-test showed that both taxa vary significantly by the following parameters ($P<5\%$): H, N, H/B, H/LA, and H/BW; the one-way-ANOVA yielded corresponding results.

The shells of the only lot from Java with precise locality data (ZMB 4.074) is identified here as *S. martini* given its elongated shell (while the original label states "*M. sulcospira*" instead). The statistical test has been employed to explore whether these shells can significantly be discriminated either from shells of *S. sulcospira* or *S. martini* in regard to shell morphometry. Comparison of shells of the lot ZMB 4.074 with shells of *S. sulcospira* (MNHN, ZMA, ZMB 200.101, ZMZ 522306) by t-test reveals that both groups differ significantly in the parameters H/LA, H/BW, and with a weak support ($P = 0.51$) for H/B, whereas no significant differences were found when comparing the lot ZMB 4.074 with other shells of *S. martini* (BMNH 19990497, RMNH 71326-8).

Table 3. Results of the discriminate analysis of shell parameters.

Predicted group membership	*S. sulcospira*	*S. martini*
S. sulcospira	25 (100.0%)	0 (0.0%)
S. martini	1 (1.7%)	59 (98.3%)

A graphic comparison of the two taxa by means of selected shell parameters is shown in Figures 25–26. Shells assigned to each of the two taxa according to their morphology were found to be correctly classified by a discriminate analysis of morphometric data with good statistical support (Table 3). It is concluded that shells of *S. sulcospira* are smaller and more conical in shape than shells of *S. martini* (Table 1, Figure 26).

DISCUSSION

I. Evaluation of Morphological Characters of *Sulcospira*

The operculum and radula of *S. sulcospira* led Troschel (1858) to describe a new genus for this species. However, among the Pachychilidae the operculum is known to be relatively conservative in its general organization (that is, to be multispiral, rounded or ovate) but quite variable in relation to their number of whorls and increase in diameter, even within a single genus (Köhler and Glaubrecht, 2001, for *Brotia*; Köhler and Glaubrecht, 2003, for *Jagora*; Glaubrecht and Rintelen, 2003, for *Pseudopotamis*; Rintelen, 2003, for *Tylomelania;* Köhler, 2003). Consequently, an operculum possessing four regular whorls might be typical for *S. sulcospira,* but only at the species level. The possession of a round to oval, multispiral operculum led Sarasin and Sarasin (1898) to group several taxa within the so-called "palaeomelanians", as contrasted with the so-called "neomelanians", which exhibit a paucispiral operculum. In fact, this grouping coincides well with the modern concept of the Pachychilidae and Thiaridae, respectively (Glaubrecht, 1996, 1999; Köhler and Glaubrecht, 2001, 2002, 2003). Therefore, operculum morphology in *S. sulcospira* corroborates the placement of the taxon within the Pachychilidae. This, however, represents a plesiomorphic character state among the representatives of this family, and is not a suitable character to establish generic distinction.

By and large, the same can be stated for the radula. The molluscan radula is generally considered a conservative character (Fretter and Graham, 1994). The pattern described and depicted by Troschel (1858) (Figure 1) is commonly found among pachychilids (Köhler and Glaubrecht, 2001, 2002, 2003; Glaubrecht and Rintelen, 2003; Rintelen and Glaubrecht, 1999, 2003). This had been already noticed by Troschel (1858), when allocating taxa such as *Pachychilus* and *Sulcospira* (but also *Me-*

lanopsis) under the "Pachychili". However, we have been unable to identify a single radular character peculiar to *Sulcospira*, based on the limited anatomical features discussed here. An enlarged main cusp is also found in other pachychilid species, such as *B. pagodula* (Köhler and Glaubrecht, 2001). Moreover, it is evident that radular characters may especially be prone to adaptation, parallelism, and convergence and that intraspecific variability and plasticity in general may be considerable, as described, e.g., for littorinid gastropods (Padilla, 1998; Reid and Mak, 1999; Reid, 2000). Thus, possession of an elongated cusp alone is not considered a characteristic suitable for the diagnosis of *Sulcospira*.

Gross anatomy of *S. sulcospira* and *S. martini* remains unknown, due to the lack of ethanol-preserved specimens. It has been shown for other pachychilids, though, that particularly characters of the reproductive organs (pallial oviduct, gonads, brooding structures) and the protoconch may bear essential systematic information (Köhler and Glaubrecht, 2001, 2003).

Juvenile shells extracted from dried adults (Troschel, 1858; and own observations) deliver circumstantial evidence that *Sulcospira* is viviparous. Furthermore, as made evident from the following comparison, the protoconchs of *S. sulcospira* are similar to those of some species we have primarily assigned to the "*Brotia-testudinaria*-group" (Köhler and Glaubrecht, 2001, e.g., *Brotia testudinaria* and *B. hainanensis*; Figures 29–30). In contrast, other taxa constituting the genus *Brotia* sensu stricto (denominated the "*Brotia pagodula* group" by Köhler and Glaubrecht, 2001) have juveniles with an irregularly wrinkled sculpture of the apical whorl of the protoconch (Figures 25–26). Protoconchs of *Tylomelania* and *Pseudopotamis* exhibit yet another fine morphology (Figures 27–34). They attain a relative large size and exhibit a relatively small apical whorl with a smooth shell as well as regularly increasing whorls (Rintelen and Glaubrecht, 1999, 2003; Glaubrecht and Rintelen, 2003).

As discussed in some detail by Köhler and Glaubrecht (2001), distinct protoconch morphologies of several pachychilid genera are correlated with different reproductive strategies. For example, *Brotia* possesses a subhaemocoelic brood pouch while representatives of *Tylomelania* and *Pseudopotamis* are characterized by an eu-viviparous mode of reproduction utilizing a modified oviduct as brood pouch (= uterine brood pouch; Rintelen and Glaubrecht, 1999; Glaubrecht and Rintelen, 2003). Females of the latter two taxa retain a small number of embryos in the uterus that are nourished by secretions produced by the albumen gland.

The protoconchs of *Sulcospira* correspond to those of the so-called "*Brotia testudinaria* group" (Köhler and Glaubrecht, 2001), which indicates to us that *S. sulcospira* possesses a subhaemocoelic brood pouch as well.

II. Comparison of *S. sulcospira* and *S. martini*

Sulcospira martini, which has tentatively been allocated to the genus by Köhler and Glaubrecht (2002), can be distinguished by its shell, but much more conspicuously by its different protoconch morphology, which is unique among the Pachychilidae.

Because the protoconch morphology is related to the mode of reproduction, it is assumed that *S. martini* exhibits reproductive features (e.g. incubatory structure, reproductive strategy) that may be distinct from those known from any other pachychilid taxon.

III. Systematic Conclusions

Shell, operculum, and radula of *S. sulcospira* (and also of *S. martini*) are typically pachychilid; a basally well rounded and flared aperture, a round to oval, multispiral operculum, and a rachidian tooth with an enlarged main cusp flanked by up to three accessory cusps that taper in size are diagnostic characters of this family. However, these characters are symplesiomorphic and, thus, uninformative at the generic level. Soft body morphology, which could bear crucial information, is not known. Still, some systematic conclusions can be drawn based on the evaluation of protoconch morphology, which is considered to be more or less constant at the generic level: First, species of *Brotia* (Figures 27–28), *Tylomelania* (Figures 31–32), and *Pseudopotamis* (Figures 33–34) are not congeneric with *S. sulcospira* (see Figures 19–20) since they exhibit each a distinct protoconch, which is testimony to a different reproductive strategy as discussed above. The same holds true for *Jagora* (Köhler and Glaubrecht, 2003). All these pachychilid genera have been shown to represent independent monophyletic lineages characterized by morphological features, such as peculiar reproductive morphologies. Second, the protoconch of *S. sulcospira* is very similar to that known from species of the "*Brotia-testudinaria*-group" denominated by Köhler and Glaubrecht (2001) (Figures 29, 30 for *B. hainanensis*). Hence, *Sulcospira* Troschel, 1858, being available and valid, might be an appropriate generic name for this species group under the precondition that it can be shown that a protoconch with a smooth and dome-shaped apical whorl is a character possessed by the members of this group and derived by shared ancestry. However, the alternative explanation that a similar protoconch represents an ancestral state that is present in two different lineages has to be ruled out. Otherwise, inferring generic relationship in absence of a phylogenetic evaluation could lead to the erection of paraphyletic taxa when the characters considered are plesiomorphic. Before we cannot show by phylogenetic analyses of morphological or molecular data that *S. sulcospira* and species of the "*Brotia testudinaria* group" indeed belong to the same taxon, we therefore refrain from a respective taxonomic suggestion.

Third, we conclude that *S. martini* can be recognized as a species and that it does not represent a synonym of *S. sulcospira*. Furthermore, it is clear that the morphology of the protoconch of *S. martini* does resemble neither of the known pachychilid genera very closely (Figures 27–34) including that of *S. sulcospira* (Figures 19–

20). Just based on this single feature, it could be deduced that *S. martini* might be a representative of a yet undescribed genus. However, as has been stated for *S. sulcospira*, a sound decision on its systematics should rely on a more comprehensive data set.

For the time being, we suggest to maintain *Sulcospira* as a monotypic genus endemic to Java. Furthermore, we refrain from a taxonomic decision on the generic relationship of *"Sulcospira" martini*. It likely is not a member of one of the described pachychilid genera, but its true relationships remain unknown.

Irrespective of our anticipation that both species dealt with in this paper may have already become extinct in large parts of their original distribution area, we still hope that suitable material will turn up, eventually allowing to find an answer to the remaining questions and to solve another of the many puzzling aspects of pachychilid phylogeny and systematics that long hampered a deeper understanding of the evolution of this intriguing and instructive case study among the lymnic Cerithioidea.

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Six new species of *Paryphantopsis* (Gastropoda: Pulmonata: Charopidae) from the Papuan Peninsula of New Guinea

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ABSTRACT

Six new species of *Paryphantopsis*, a genus of charopid snails endemic to New Guinea, are described from the geologically complex eastern terminus of the Papuan Peninsula. All descriptions are based on material collected in 2002–2003 and include information on shell, genital, and radular anatomy. Of the 14 previously described species, genital anatomy was known for three and radular morphology for only one species. Examination of these under-utilized character sets has uncovered taxonomically useful interspecific variation. The six new species appear to have distributions limited to particular mountain groups on the extreme eastern terminus of the Papuan Peninsula. Species in close proximity or sympatry share unique shell, genital and radular characters suggesting local speciation and poor dispersal ability. Diversity in *Paryphantopsis* has been underestimated and it is likely that there are many species yet to be discovered with narrow geographic and ecological ranges in the under-explored mountains of New Guinea.

INTRODUCTION

Paryphantopsis, a genus of charopid snails endemic to New Guinea, are found at moderate and high altitudes (600–4000 m) and are distributed from Western Papua (Irian Jaya) to the Louisiade Archipelago. The genus contains fourteen previously described species: *P. arcuata* Jutting, 1964, *P. dualoensis* Solem, 1970, *P. elegans* (Fulton, 1902), *P. filosa* Jutting, 1964, *P. fultoni* (Coen, 1922), *P. globosa* (Hedley, 1890), *P. lamelligera* (Thiele, 1928), *P. latior* Jutting, 1964, *P. louisiadarum* (Möllendorff, 1899), *P. platycephala* Jutting, 1964, *P. pygmaea* (Bavay, 1908), *P. sculpturata* Jutting, 1964, *P. similis* (Thiele, 1928), and *P. striata* (Fulton, 1902). Solem (1970) reviewed the genus, redescribing all species except those then recently described or reviewed by Jutting (1964). Most *Paryphantopsis* species are known from small samples of shells, often only from their type localities, and data on genital morphology are limited to three species, and on radular morphology to only one species (Solem, 1970, Wiktor, 2003). *Paryphantopsis* has not been reported previously east of longitude 148° E on the relatively poorly sampled eastern part of New Guinea, which is known as the Papuan Peninsula. The eastern end of the peninsula includes the Cloudy Mountains to the south, and the disjunct terminus of the Owen Stanley Range to the north, separated from the main Owen Stanley uplands by extensive lowlands west of Mount Suckling. The geologically complex Papuan Peninsula is formed largely by the East Papua Composite Terrane (EPCT), a tectonic province composed of at least 4 separate geological units with differing ages, origins, and histories. These units appear to have assembled northeast of modern New Guinea during the Paleocene, 62–57 Myr ago, and fused to the main body of the island in the Late Oligocene to Early Miocene, 28–22 Myr ago (Pigram and Davies, 1987). Because of its likely initial offshore amalgamation, the EPCT may have developed a distinct and largely endemic biota. This is the first in a series of papers describing the results of ten weeks of field surveys that took place during April–May, 2002 and January–March, 2003. These surveys explored the extreme eastern terminus of the Papuan Peninsula where two geological units lie in close proximity, the Cloudy Mountains of the Port Moresby Terrane and eastern terminus of the Owen Stanley Range of the Kutu Terrane (Figure 1).

MATERIALS AND METHODS

Specimens were hand-collected or sifted from samples of leaf-litter. Live collected animals were drowned overnight and then preserved in 75% ethanol. Gross anatomical dissections were made under 75% ethanol using a dissecting microscope. Radulae were isolated from dissected buccal masses using a saturated KOH solution. Scanning electron micrographs of radulae were made using a field emission SEM. Drawings of the genital anatomy were made with the assistance of a *camera lucida*, and measurements were taken using an ocular micrometer. Shell measurements were made as follows. Whorl count (W) was measured from the suture of the first whorl to the body whorl and fractions of a whorl were determined with the aid of a cardboard circle divided into 10 equal parts of 36° (Figure 2, line 1–2.9). Spire

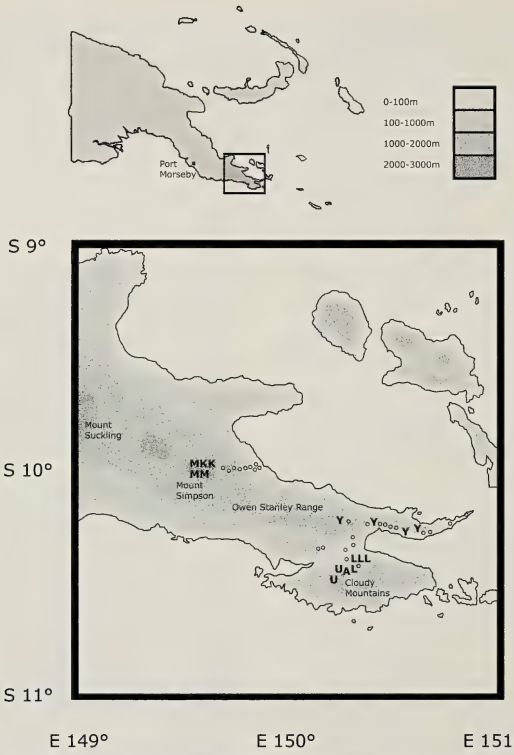
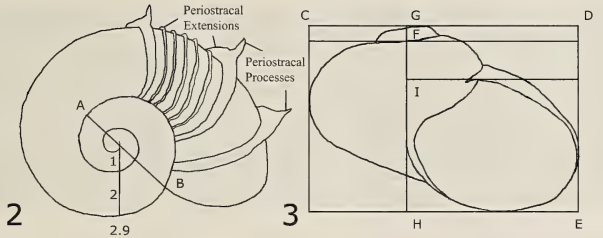


Figure 1. Distribution of *Paryphantopsis* on the eastern terminus of the Papuan Peninsula, Papua New Guinea between 9° S, 149° E and 11° S, 151° E. A = *P. abstrusa*, K = *P. koragae*, L = *P. lebasii*, M = *P. matawanensis*, U = *P. ubwamensis*, Y = *P. yawii*, O = other sites sampled.

diameter (SD) was the length of a straight line passing from the apertural edge of the suture through the middle of the apex to the opposite suture (Figure 2, line A–B). Diameter (D) was the greatest width of the shell perpendicular to the shell axis (Figure 3, line C–D). Height (H) was the greatest distance between the apex and the base of the aperture measured parallel to the shell axis (Figure 3, line D–E). Spire height (SH) was measured from the top of the body whorl to the apex of the shell (Figure 3, line F–G). Aperture width (AW) was the greatest distance from the columellar edge to the outer edge of the aperture (Figure 3, line E–H). Aperture height (AH) was measured from the suture to the base of the aperture, parallel to the shell axis (Figure 3, line H–I). The lengths of radular teeth were measured from the top of the mesocone to the posterior edge of the basal plate. The widths of radular teeth were measured as the greatest width of the cusps, not the basal plate. The following abbreviations are used in figures of genital anatomy: AT = atrium, DI = diverticulum, EP = epiphallus, OV = free oviduct, PE = penis, PG = prostate gland, PP = penial pilasters, PR = penial retractor muscle, SD = spermathecal duct, SP = spermatheca, VA = vagina, VD = vas deferens, VP = vergic



Figures 2–3. Diagram of shell measurements. **2.** Whorl count (line 1–2.9), spire width (line A–B). **3.** Diameter (line C–D), height (line D–E), spire height (line F–G), aperture width (line E–H), aperture height (line H–I).

papillae. Specimens are deposited in the following institutions: Bernice P. Bishop Museum, Honolulu (BPBM), Florida Museum of Natural History, Gainesville (UF), Papua New Guinea National Museum, Port Moresby (PNGNM), Wroclaw University Museum of Natural History (MNHW).

SYSTEMATICS

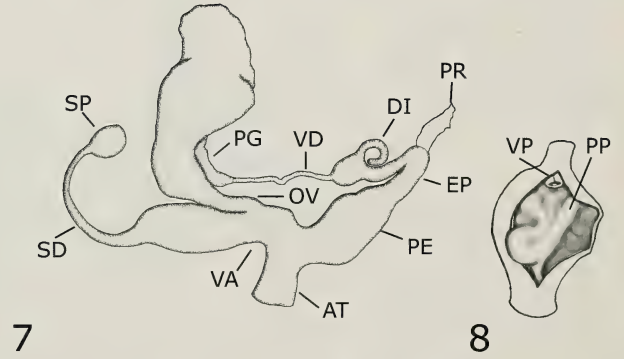
Family Charopidae Hutton, 1884
Genus *Paryphantopsis* Thiele, 1928 (Type species: *Flammulina* (*Paryphantopsis*) *lamelligera* Thiele, 1928, by original designation.)

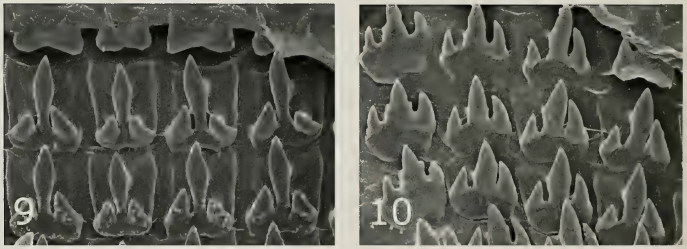
Description: Moderate to large-sized charopid snails with loosely coiled shells of approximately three whorls. Shell shape varies among species from globose to depressed with an elevated to flat spire and a rounded to keeled margin. The umbilicus, usually covered by an expansion of the peristome, is sometimes perforate. Nuclear whorls (protoconch) are sculptured with spiral rows of small pits that become weaker and less regular on later whorls. Postnuclear whorls (teleoconch) are usually sculptured with growth lines accentuated with short periostracal extensions punctuated with occasional longer extensions at regular intervals. These longer extensions can bear additional processes at the shell margin (Figure 2). A few species do not have longer periostracal extensions and some species do not bear any extensions. Body color is usually yellow in life. The epiphallus is apically inflated, often with an apical diverticulum. The penis is textured with convoluted pilasters of varying complexity. Central teeth of the radula are tricuspid and of similar size to the tricuspid and slightly assymetrical lateral teeth. The many lateral teeth become shorter and less symmetrical, grading in shape with the marginal teeth. Marginal teeth are usually assymetric, their endocones longer than their ectocones. Endocones and ectocones and less often mesocones can bear accessory cusps.

Paryphantopsis abstrusa new species
(Figures 4–10, Table 1)

Description: The adult shell is small for the genus, 4.4–4.8 mm (mean = 4.6) in diameter and 3.5–3.8 mm (mean = 3.6) in height, with 2.9–3.0 (mean = 3.0) rapidly expanding whorls (Figures 4–6, Table 1). The spire is elevated 0.3 mm. Postnuclear whorls descend regularly and the shell height/diameter ratio is 0.76–0.81 (mean = 0.79). The shell has 1.3 evenly rounded nuclear whorls, sculptured with 12 spiral rows of small pits. The postnuclear whorls bear weak and irregular malleations, most readily visible at the base, and indistinct and irregular striae on the apical surface. The postnuclear whorls are also sculptured with weak growth lines. Approximately every fourth growth line is accentuated by a periostracal extension. The periostracal extensions bear small (0.15 mm) trigonal processes at the periphery. These processes occur on every periostracal extension for the first two whorls, then become less regular and finally absent from the final ½ whorl. The fragile processes are often partially worn from the earlier whorls of adult shells. The nuclear whorls are white, the postnuclear whorls brown. The umbilicus is closed by a reflection of the peristome. The aperture is large, ovate to nearly circular, with an aperture-diameter to aperture-height ratio of 0.54–0.67 (mean = 0.63).

The body color is uniform bright yellow-white in life, fading to cream in specimens preserved in ethanol. The vas deferens narrows rapidly from the prostate gland and remains narrow to the swollen head of the epiphallus (Figure 7). A long coiled diverticulum inserts laterally on the epiphallus soon after the junction with the vas deferens. The epiphallus narrows slightly after the diverticulum and widens towards the junction with the penis. The penis is half the length and three times the width of the epiphallus, robust, widest centrally, and narrowing slightly at each end. Apically there are several small convoluted pilasters and one much larger convoluted pilaster that extends to near the base (Figure 8). The penial retractor muscle is robust, originating from





Figures 4–10. *Paryphantopsis abstrusa*. **4–6.** Photographs of shell, Holotype UF 308235, diameter 4.6 mm. **7–8.** Camera lucida drawing of genitalia, UF 299677, maximum width 7.2 mm. **9–10.** Scanning electron micrograph of radula, UF 299677, field width of central and lateral teeth 41 μm, marginal teeth 42 μm.

Table 1. Measurements in mm of undamaged adult shells of six species of *Paryphantopsis*, N = count, H = height, D = diameter, SH = spire height, SD = spire diameter, AH = aperture height, AD = aperture diameter, W = number of whorls.

Species	N		H	D	SH	SD	AH	AD	W
P. abstrusa	3	mean ± SD	3.6 ± 0.2	4.6 ± 0.2	0.3 ± 0.0	2.1 ± 0.0	2.6 ± 0.2	2.8 ± 0.1	3.0 ± 0.1
		range	3.5–3.8	4.4–4.8	0.3–0.3	2.0–2.1	2.4–2.7	2.7–2.9	2.9–3.0
P. koragae	3	mean ± SD	2.9 ± 0.1	4.2 ± 0.0	0.2 ± 0.0	1.6 ± 0.1	2.1 ± 0.1	2.6 ± 0.1	2.8 ± 0.1
		range	2.8–3.0	4.1–4.2	0.1–0.2	1.5–1.7	2.0–2.1	2.5–2.7	2.7–2.8
P. lebasii	41	mean ± SD	3.6 ± 0.2	6.8 ± 0.5	0.1 ± 0.1	2.5 ± 0.2	2.8 ± 0.2	4.3 ± 0.4	2.8 ± 0.1
		range	3.3–4.0	6.1–7.5	0.0–0.2	2.3–2.8	2.4–3.0	3.9–4.9	2.7–2.9
P. matawanensis	5	mean ± SD	4.5 ± 0.5	7.0 ± 0.4	0.1 ± 0.1	2.6 ± 0.3	3.6 ± 0.5	4.5 ± 0.4	2.9 ± 0.2
		range	4.0–4.9	6.6–7.3	0.0–0.1	2.2–2.8	3.2–4.1	4.1–4.8	2.7–3.0
P. ubwamensis	3	mean ± SD	5.0 ± 0.2	7.1 ± 0.7	0.3 ± 0.1	3.0 ± 0.3	3.8 ± 0.3	4.3 ± 0.5	3.0 ± 0.1
		range	4.8–5.1	6.4–7.7	0.2–0.4	2.7–3.3	3.6–4.1	3.9–4.9	2.9–3.1
P. yawii	55	mean ± SD	3.1 ± 0.3	5.9 ± 0.4	0.2 ± 0.1	2.2 ± 0.3	2.3 ± 0.3	3.7 ± 0.4	2.7 ± 0.1
		range	2.6–3.6	5.0–6.5	0.1–0.3	1.9–2.6	2.0–2.7	3.2–4.1	2.6–2.8

the diaphragm and inserting at approximately mid-point on the epiphallus. The spermathecal duct is robust, narrowing abruptly at mid-point and remaining narrow until joining the relatively small, ovate spermatheca. The free oviduct joins the moderate length vagina above the atrium.

The central teeth of the radula (second row from left) are tricuspid, 8–9 μm wide and 11–12 μm long, roughly the same shape as, but smaller than, the first lateral teeth, which are 9–10 μm wide and 12–13 μm long (Figure 9). The mesocones of both the central and first lateral teeth are tall, slender, and blade-shaped, joining the rectangular basal plates close to, but not on, their posterior edge. The mesocones of the central teeth barely project beyond the anterior edge of the basal plates, those of the lateral teeth project well beyond the edge. The ectocones are trigonal and short only one third of the height of the mesocones, joining the posterior edge of the basal plates. The lateral teeth are asymmetrical, their endocones are slightly taller then their ectocones. The marginal teeth are dorsoventrally compressed and tricuspid to multicuspid, 8–9 μm wide and 11–12 μm long (Figure 10). The endocones of the marginal teeth are half the height of the mesocones and only slightly taller than the ectocones. The mesocones of the marginal teeth often bear small cusps near the mid-point.

Type Material: Holotype: UF 308235, J. Slapcinsky, 16 April 2002; Paratypes: UF 299667 (2 specimens), UF 303588 (4 specimens), type locality, J. Slapcinsky, 16 April 2002.

Type Locality: Papua New Guinea, Milne Bay Province, Cloudy Mountains, Ubwam Mountain, headwaters of the Watuti River, 10° 29.8′ S, 150° 14.02′ E, 670 m altitude.

Habitat: Observed crawling near the base of trees with smooth bark, in native forest, during wet weather at 670 meters altitude.

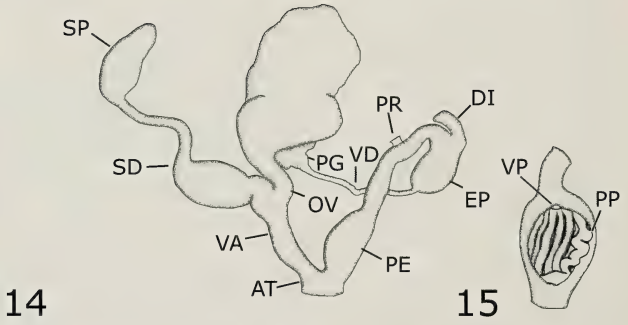
Etymology: From the Latin *abstrusa,* a feminine adjective meaning hidden, concealed and reserved, alluding to the difficulty finding this species and to its subtle almost concealed periostracal processes.

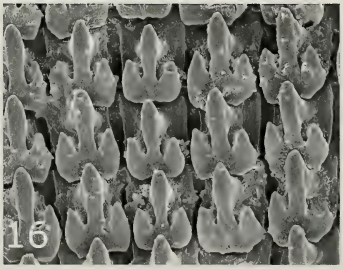
Remarks: *Paryphantopsis abstrusa* differs from most other *Paryphantopsis* smaller than 5 mm in diameter by having periostracal extensions with processes at their margins. *Paryphantopsis similis* is the only other small species with periostracal extensions. It is more depressed, with a height/diameter ratio of 0.70 compared to a height/diameter ratio of 0.79 in *P. abstrusa.*

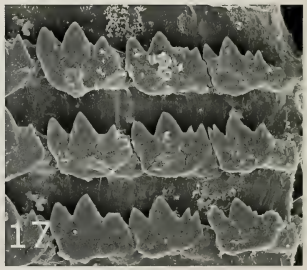
Paryphantopsis koragae new species
(Figures 11–17, Table 1)

Description: The adult shell is small for the genus, 4.1–4.2 mm (mean = 4.2) in diameter and 2.8–3.0 mm (mean = 2.9) in height, with 2.7–2.8 (mean = 2.8) rapidly expanding whorls (Figures 11–13, Table 1). The spire is slightly elevated, 0.1–0.2 mm (mean = 0.2), postnuclear whorls descend slowly and regularly. Shell height/diameter ratio is 0.67–0.71 (mean = 0.69). There are 1.1 evenly rounded nuclear whorls, sculptured with 12 spiral rows of small pits that are not continued on the postnuclear whorls. The postnuclear whorls have regular growth wrinkles with irregular, short, periostracal extensions that are slightly weaker basally. None of the periostracal extensions extend further than the others. The nuclear whorls are white, the postnuclear whorls are dark brown. The umbilicus is closed by a reflection of the peristome. The aperture is large, flattened apically and slightly angled at the periphery and base of the columella. The aperture-diameter to aperture-height ratio is 0.78–0.80 (mean = 0.79).

The body color is uniform yellow in life, fading to cream in specimens preserved in ethanol. The vas deferens narrows rapidly after the prostate gland and remains narrow until entering the swollen, ovate head of the epiphallus (Figure 14). The interior of the head of the epiphallus bears two strong pilasters that enter the short broad diverticulum, which is roughly one quarter of the length of the epiphallus. The epiphallus is two to three times longer than the penis and one third narrower







Figures 11–17. *Paryphantopsis koragae.* **11–13.** Photographs of shell, Holotype UF 308237, diameter 4.2 mm. **14–15.** Camera lucida drawing of genitalia, UF 303586, maximum width 6.3 mm. **16–17.** Scanning electron micrograph of radula, UF 303586, field width of central and lateral teeth 55 μm, marginal teeth 41 μm.

at the junction with the penis. The very short penial retractor muscle originates on the diaphragm and inserts near the mid-point of the epiphallus. The interior of the penis bears several smooth, low, regular pilasters and one much larger convoluted pilaster (Figure 15). The spermatheca is oblong-ovate, its duct is apically narrow and widens abruptly at the mid-point. The free oviduct is relatively robust, joining the long vagina well above the atrium.

The central teeth of the radula (center row) are tricuspid, 9–10 μm wide and 12–13 μm long, slightly smaller than the first lateral teeth, which are 10–11 μm wide, 13–14 μm long (Figure 16). The mesocones of both central and lateral teeth barely project beyond the basal plate. The ectocones of the central and lateral teeth are about one half the height of the mesocones. The lateral teeth are tricuspid and very slightly assymetric with the endocone of each lateral slightly taller than the ectocone. The marginal teeth are dorsoventrally compressed and tricuspid or weakly and irregularly multicuspid, 8–13 μm wide and 8–10 μm long (Figure 17). The endocones of the marginal teeth are nearly the height of the mesocones and can have very weak secondary cusps; the ectocones are shorter and unicuspid to irregularly multicuspid.

Type Material: Holotype: UF 308237, J. Slapcinsky, 20 February 2003; Paratypes: Papua New Guinea, Milne Bay Province, Mount Matawan (Mount Simpson): UF 303586 (2 specimens), UF 303587 (2 specimens), type locality; UF 303584 (1 specimen), plateau ENE of summit, 10°2.1′ S, 149°34.6′ E, 2567 m altitude, J. Slapcinsky, 17 February 2003; UF303585 (1 specimen), Bunisi Village, 10°1.1′ S, 149°36.2′ E, 1450 m altitude, J. Slapcinsky, 16 February 2003.

Type Locality: Papua New Guinea, Milne Bay Province, Mount Matawan (Mount Simpson): NE of summit, 10°1.7′ S, 149°34.7′ E, 2100 m altitude.

Habitat: Active on plants and leaf litter usually near the ground. Observed aestivating in suspended leaf litter within 1.5 m of the ground in tropical hardwood forest and cloud forest from 1450 m to 2600 m altitude.

Etymology: This matronym honors Ms. Helen Korage, Councelor for the Village of Ikara, who facilitated our access to the Mount Matawan area.

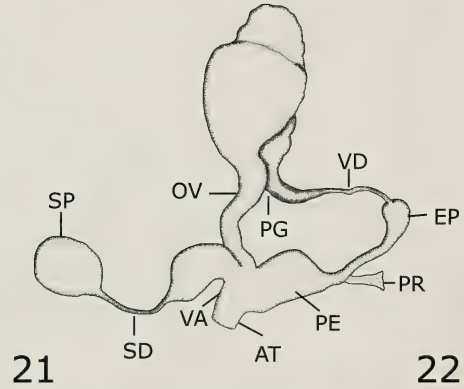
Remarks: *Paryphantopsis koragae* differs from other species of *Paryphantopsis* in being sculptured with growth lines accentuated with very short periostracal extensions. All other small species (≤ 5 mm diameter), including *P. filosa, P. pygmaea, P. arcuata, P. sculpturata, P. similis, P. platycephala,* and *P. abstrusa* have occasional longer periostracal extensions. The anatomy of only one *Paryphantopsis* species of similar size has been figured previously: *P. filosa* from Karkar Island near Madang (Wiktor, 2003, fig. 9). This species differs from *P. koragae* in not having a diverticulum on the epiphallus.

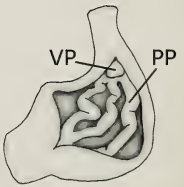
Paryphantopsis lebasii new species
(Figures 18–24, Table 1)

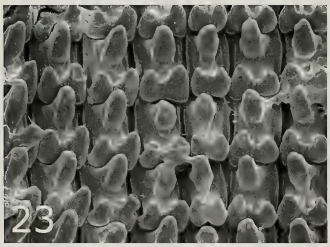
Description: The adult shell is slightly larger than average for the genus, 6.1–7.5 mm (mean = 6.8) in diameter and 3.3–4.0 mm (mean = 3.6) in height, with 2.7–2.9 (mean = 2.8) rapidly expanding whorls (Figures 18–20, Table 1). The spire is flat to slightly elevated, 0.0–0.2 mm (mean = 0.1). Postnuclear whorls descend slowly and regularly and shell height/diameter ratio is 0.45–0.61 (mean = 0.53). There are 1.3 nuclear whorls, with weak, peripheral and supraperipheral angles, and sculptured with about 12 spiral rows of small pits. These pits become larger and less regular on the postnuclear whorls, where they are visible through the periostracum as weak malleations. The sculpture of spiral rows of oblong pits is clearer where the periostracum is removed. The shell periphery is weakly keeled. Apical surface of the whorls is broadly rounded or with a very weak supraperipheral angle. Regular growth wrinkles accentuated with short periostracal extensions are present on the postnuclear whorls. On the apical surface, these extensions are folded along their length towards the aperture and are weakly appressed to the shell. Approximately every fifth periostracal extension protrudes about 0.5 mm beyond the shell margin forming large rectangular processes. These processes overlap each other on the penultimate whorl, but not on the body whorl. They are approximately equally spaced, rectangular, distally rounded, and of approximately equal length. Periostracal extensions of the growth lines are shorter, erect, and less prominent basally. Nuclear whorls are white; postnuclear whorls pale yellow brown. The umbilicus is perforate or, less often, closed, covered to varying degrees by a reflection of the peristome. The aperture is large, depressed-ovate with an aperture-diameter to aperture-height ratio of 0.51–0.75 (mean = 0.65).

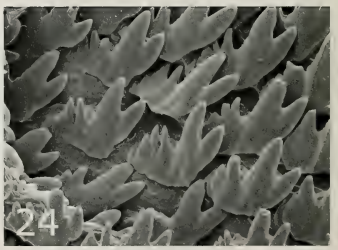
The body color is uniform bright creamy-yellow in life, fading to creamy-white in specimens preserved in ethanol. The vas deferens narrows to the junction with the ovate head of the epiphallus (Figure 21). The epiphallus is approximately one quarter the diameter of the penis and does not bear a diverticulum. The penial retractor muscle is a little less than half the length of the epiphallus, originating from the diaphragm and inserting at the base of the epiphallus. The robust penis is a little shorter than the epiphallus, with three strong pilasters that run its entire length (Figure 22). The atrium is short, expanding slightly toward the junction with the penis and vagina. The spermathecal duct is massive at the base, tapering rapidly at mid point, the remainder is relatively narrow until its junction with the spherical spermatheca. The free oviduct is slightly coiled and narrow, joining the very short vagina just above the atrium.

The central teeth of the radula (fifth row from left) are symmetrically tricuspid, 8–9 μm wide and 13–14 μm long, and are similar in shape and length to the slightly wider (9–10 μm), and slightly asymmetrical lateral teeth (Figure 23). The bluntly conical and erect mesocones of









Figures 18–24. *Paryphantopsis lebasii.* **18–20.** Photographs of shell, Holotype UF 308233, diameter 6.5 mm. **21–22.** Camera lucida drawing of genitalia, UF 299671, maximum width 6.7 mm. **23–24.** Scanning electron micrograph of radula, UF 299671, field width of central and lateral teeth 67 μm, marginal teeth 38 μm.

the central and lateral rows join their basal plates centrally and barely project beyond the anterior of their basal plates. The ectocones of both the central and lateral rows are trigonal and short, about half the height of the mesocones; they join the posterior edge of their basal plates at a low buttress. The endocones of the lateral teeth are slightly larger but otherwise of similar shape to their ectocones. The marginal teeth are dorsoventrally compressed, multicuspid, about 9–10 μm wide and 10–11 μm long (Figure 24). The endocones are nearly the same height as the mesocones while the ectocones are much shorter, about one half to one third the height of the mesocones and divided into three cusps.

Type Material: Holotype: UF 308233, J. Slapcinsky, 9 April 2002; Paratypes: Papua New Guinea, Milne Bay Province: UF 299676 (1 specimen); UF 299699 (5 specimens), Cloudy Mountains, Ubwam Mountain, headwater of the Watuti River, 10°29.8′ S, 150°14.0′ E, 675 meters altitude, J. Slapcinsky, 16 April 2002; UF 299674 (8 specimens); UF 303593 (4 specimens), Pini Range, Duabo Mission Station, 10°25′ 05″ S, 150°18′ 24 E, 325 meters altitude, J. Slapcinsky, 9 April 2002; BPBM (2 specimens); MNHW 978 (2 specimens); PNGNM 004-105 (2 specimens); UF 299671 (19 specimens); UF 303591 (1 specimen), 30 April 2002; UF 303590 (7 specimens), 2 March 2003, Pini Range, E of Duabo Mission Station, 10°25.0′ S, 150°18.6′ E, 325 meters altitude, J. Slapcinsky; UF 299677 (1 specimen), 30 April 2002; UF 303592 (1 specimen), 1 May 2002, Pini Range, abandoned logging road W of Duabo Mission Station, 10° 24.9′ S, 150° 18.3′ E, 325 meters altitude, J. Slapcinsky.

Type Locality: Papua New Guinea, Milne Bay Province, Pini Range, Duabo Mission Station, 10°25′ 04.7″ S, 150°18′ 24.4″ E, 325 meters altitude.

Habitat: Found on logs, mossy rocks and wet ground, usually near streams in disturbed and undisturbed broadleaf forest in hilly terrain from 325 to 700 meters altitude. Observed active during the day.

Etymology: This patronym honors Mr. Biga Lebasi, our host and guide at Duabo Mission Station, the type locality.

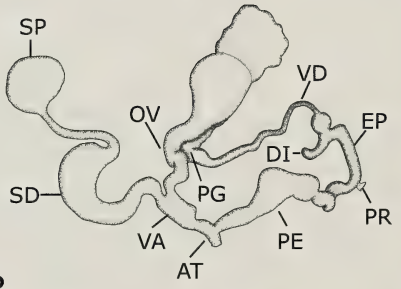
Remarks: Only four other *Paryphantopsis* species, *P. elegans, P. fultoni, P. yawii,* and *P. lamelligera* have weak to strong peripheral keels. *Paryphantopsis lebasii* is unlike all species *except P. yawii* and *P. fultoni,* in having large, rectangular periostracal extensions oriented parallel to the keeled shell margin. These peripheral extensions are all of equal length, unlike in *P. fultoni,* and do not overlap on the body whorl, unlike in *P. yawii.*

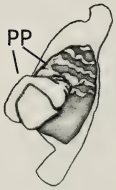
Paryphantopsis matawanensis new species
(Figures 25–31, Table 1)

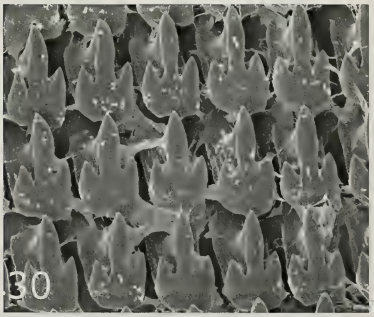
Description: The adult shell is larger than average size for the genus, 6.6–7.3 mm (mean = 7.0) in diameter and 4.0–4.9 mm (mean = 4.5) in height, with 2.7–3.0 (mean = 2.9) rapidly expanding whorls (Figures 25–27, Table 1). The spire is flat or very slightly elevated, 0.0–0.1 mm (mean = 0.1). Postnuclear whorls descend regularly and shell height/diameter ratio is 0.61–0.69 (mean = 0.64). There are 1.3 rounded nuclear whorls, sculptured with 6 spiral rows of small pits that grade into weak, spiral striae on the penultimate whorl; shell sculpture is obscured by periostracum on the body whorl. The shell is wider and slightly angular below the mid-point. The postnuclear whorls have regular growth wrinkles accentuated with low periostracal extensions that alternate with several much longer extensions approximately every 10 growth-lines. The grouping of several longer extensions appears like a single very thick periostracal extension to the naked eye. The nuclear whorls are white, the postnuclear whorls are dark brown to red-brown. A reflection of the peristome closes the umbilicus. The aperture is large, depressed-ovate, with an aperture-diameter to aperture-height ratio of 0.54–0.67 (mean = 0.63).

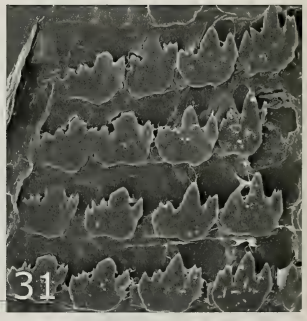
In life the body color is bright-yellow with lateral patches of dark purple-brown, the yellow fades to cream in specimens preserved in ethanol. The vas deferens narrows toward the junction with the inflated spherical head of the epiphallus. Immediately after, and perpendicular to the head of the epiphallus, there is a finger-shaped diverticulum that is roughly one quarter the length, and slightly narrower than the diameter of the epiphallus (Figure 28). The remainder of the epiphallus is somewhat twisted and approximately the same length as the penis. The penial retractor muscle is short, originating from the diaphragm and inserting on the basal third of the epiphallus. The epiphallus is roughly half the diameter of the penis. The penis expands for its apical third and then tapers basally to its junction with the similarly sized atrium. The penis apex bears several regular pilasters oriented perpendicular to the length of the penis (Figure 29). At the penis mid-point there is one very large and convoluted pilaster that extends basally. The wall of the base of the penis is thin, bearing regular small pustules. The atrium is short and narrow expanding slightly towards the junction with the penis and the long vagina. The base of the spermathecal duct is relatively narrow, about the same diameter as the base of the penis and free oviduct; it triples in size to its mid-point then narrows abruptly for the remaining third before joining the spherical spermatheca. The free oviduct is narrow, joining the long vagina well above the atrium.

The central teeth of the radula (center row) are tricuspid, 11–12 μm wide and 18–19 μm long, roughly the same size and shape as the first lateral teeth (Figure 30). The mesocones of both the central and first lateral teeth are tall and sharp, tapering apically and narrowing basally. Mesocones are attached to their basal plates along their entire length, except for their apical quarter that extend beyond the anterior margin of the basal plates. The ectocones of the central teeth and the symmetric ectocones and endocones of the lateral teeth are trigonal, about half the height of the mesocones. The mar-









Figures 25–31. *Paryphantopsis matawanensis.* **25–27.** Photographs of shell, Holotype UF 308236, diameter 7.3 mm. **28–29.** Camera lucida drawing of genitalia, UF 303581, maximum width 11.7 mm. **30–31.** Scanning electron micrograph of radula, UF 303581, field width of central and lateral teeth 63 μm, marginal teeth 59 μm.

ginal teeth are dorsoventrally compressed and irregularly multicuspid, 11–12 μm wide and 10–12 μm long (Figure 31). The ectocones of the marginal teeth are slightly shorter than their endocones, which are slightly shorter than their mesocones. Both the ectocones and endocones are irregularly multicuspid, the mesocones are broadly trigonal to broadly rounded.

Type Material: UF 308236, J. Slapcinsky, 19 February 2003; Paratypes: Papua New Guinea, Milne Bay Province, Mount Matawan (Mount Simpson): UF 303581 (9 specimens), UF 303582 (3 specimens), type locality; UF 306529 (1 specimen), NE of summit, 10°2.1′ S, 149°34.4′ E, 2700 m altitude, J. Slapcinsky, 18 February 2003; UF 303583 (1 specimen), NE of summit, 10°1.7′ S, 149°34.7′ E, 2100 m altitude, J. Slapcinsky, 20 February 2003.

Type Locality: Papua New Guinea, Milne Bay Province, Mount Matawan (Mount Simpson), ridge top E of summit, 10°2.5′ S, 149°34.6′ E, 2700 m altitude.

Habitat: All specimens were collected in cloud forest from 2100 to 2700 m altitude. Individuals were observed from 1–2 m above ground, crawling on a variety of cloud forest vegetation in wet or foggy weather. In drier weather specimens were observed in leaf litter that was suspended in trees, especially in the crowns of *Pandanus* sp.

Etymology: Named for the type locality and known range of this species: Mount Matawan (Mount Simpson).

Remarks: Of the other larger (>6 mm diameter) species of *Paryphantopsis, P. globosa,* and *P. louisiadarum* do not have periostracal extensions on the growth lines, unlike *P. matawanensis.* Of the species with periostracal extensions, *P. latior, P. lamelligera, P. fultoni,* and *P. striata* do not have a repeating pattern of approximately 10 short periostracal extensions followed by several longer extensions. *P. matawanensis* further differs from *P. lamelligera* and *P. fultoni* in not having peripheral processes on the periostracal extensions. The genital anatomy of *P. matawanensis* differs from *P. lamelligera* in having a diverticulum.

Paryphantopsis ubwamensis new species
(Figures 32–38, Table 1)

Description: The adult shell is large for the genus, 6.4–7.7 mm (mean = 7.1) in diameter and 4.8–5.1 mm (mean = 5.0) in height, with 2.9–3.1 (mean = 3.0), rapidly expanding whorls (Figures 32–34, Table 1). The spire is elevated, 0.2–0.4 mm (mean = 0.3), the postnuclear whorls descend relatively rapidly, especially near the aperture. The shell height/diameter ratio is 0.66–0.75 (mean = 0.70). The 1.2 nuclear whorls are evenly rounded and sculptured with 12 spiral rows of small pits. These pits do not continue on the postnuclear whorls, which are sculptured only with weak growth lines that do not bear periostracal extensions. The whorls are inflated, the sutures deeply impressed, and the periphery evenly rounded. The nuclear whorls are white, the postnuclear whorls brown, with irregular lighter patches. The umbilicus is perforate, narrowed by a reflection of the peristome. The aperture is large, ovate, with an aperture-diameter to aperture-height ratio of 0.79–0.93 (mean = 0.85).

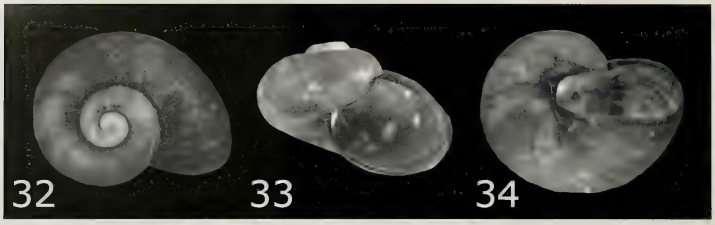
The body color is uniform yellow in life, fading to cream in specimens preserved in ethanol. The vas deferens is wide at the prostate gland, narrowing rapidly and remaining narrow until the junction with the inflated ovate tip of the epiphallus (Figure 35). The epiphallus bears a long (approximately a quarter of the length of the epiphallus), finger-shaped diverticulum just after the junction with the vas deferens. The epiphallus is about one third the diameter of the apex of the penis. The penis is broad apically, narrowing abruptly to half its apical diameter slightly before mid-point and remaining the same diameter to the junction with the atrium. The penis is sculptured with several slightly convoluted pilasters that extend in an arc from near basally to near apically, and one much larger and more convoluted pilaster near the penis mid-point (Figure 36). The penial retractor muscle originates from the diaphragm and inserts at the mid-point of the epiphallus. The spermathecal duct is basally robust and narrows at mid-point, remaining narrow until the junction with the spherical spermatheca. The free oviduct is narrow joining the moderate length vagina above the atrium.

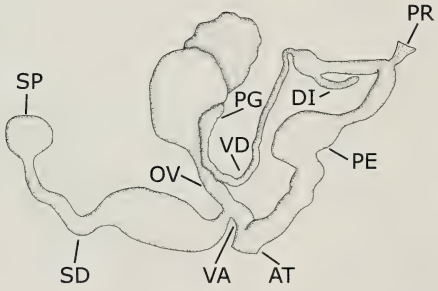
The central teeth of the radula (center row) are tricuspid, 10–11 μm wide and 15–16 μm long, roughly the same width and shape as, but a little shorter than, the first lateral teeth, which are 18–19 μm long (Figure 37). The mesocones of both the central and lateral teeth are long, slender and blade shaped, projecting slightly beyond the basal plate. The ectocones and endocones of the lateral teeth are symmetrical and half the height of the mesocones. The marginal teeth are dorsoventrally compressed and irregularly tricuspid-multicuspid, 12–15 μm wide and 13–15 μm long (Figure 38). The endocones are tall, large to very large and sometimes irregularly multicuspid. The ectocones are unicuspid.

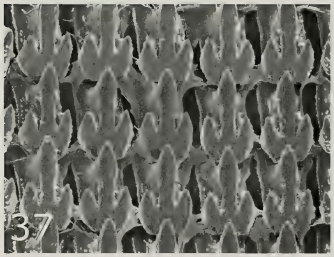
Type Material: Holotype: UF 303589, J. Slapcinsky, 22 April 2002; Paratypes: Papua New Guinea, Milne Bay Province, Cloudy Mountains, Ubwam Mountain: UF 299666 (1 specimen), type locality; UF 299668 (2 specimens), headwaters of the Watuti River, 10°29.8′ S, 150°14.02′ E, 670 m altitude, J. Slapcinsky, 16 April 2002.

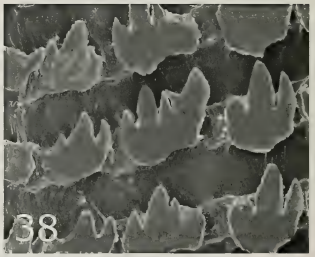
Type Locality: Papua New Guinea, Milne Bay Province, Cloudy Mountains, Ubwam Mountain, summit, 10°30.4′ S, 150°13.5′ E, 1000 m altitude.

Habitat: This species was found crawling on a moss-covered rotting log in cloud forest at 1000 meters. Dead shells were also found at 670 meters in leaf litter at the base of a tree with smooth bark.









Figures 32–38. *Paryphantopsis ubwamensis.* **32–34.** Photographs of shell, Holotype UF 303589, diameter 7.7 mm. **35–36.** Camera lucida drawing of genitalia, UF 299666, maximum width 10.1 mm. **37–38.** Scanning electron micrograph of radula, UF 299666, field width of central and lateral teeth 66 μm, marginal teeth 45 μm.

Etymology: This species is named for the type locality, Ubwam Mountain, and indirectly for one of our guides who is named after the mountain.

Type Material: Holotype: Papua New Guinea, Milne Bay Province, Cloudy Mountains, Ubwam Mountain, summit, 10°30.4′ S, 150°13.5′ E, 1000 m altitude, J. Slapcinsky, 22 April 2002 (UF 303589); Paratypes: Papua New Guinea, Milne Bay Province, Cloudy Mountains, Ubwam Mountain: type locality (UF 299666, 1 specimen); headwaters of the Watuti River, 10°29.8′ S, 150°14.02′ E, 670 m altitude, J. Slapcinsky, 16 April 2002 (UF 299668, 2 specimens).

Paryphantopsis yawii new species
(Figures 39–45, Table 1)

Description: The adult shell is average in size for the genus, 5.0–6.5 mm (mean = 5.9) diameter, and 2.6–3.6 mm (mean = 3.1) height with 2.6–2.8 (mean = 2.7) rapidly expanding whorls (Figures 39–41, Table 1). The spire is elevated, 0.1–0.3 mm (mean = 0.2). Postnuclear whorls descend slowly and regularly. Shell height/diameter ratio is 0.47–0.55 (mean = 0.53). The 1.2 nuclear whorls bear rounded peripheral and supraperipheral ridges; sculptured with about 15 spiral rows of small pits. These pits become larger and less regular on postnuclear whorls but usually are obscured by the periostracum. However, pits are visible in areas where the periostracum is removed, and within the aperture. The shell has a peripheral keel and blunt supraperipheral ridge; the surface between is flattened. Postnuclear whorls are sculptured with regular growth wrinkles that are accentuated with periostracal extensions. On the apical surface of the shell, periostracal extensions are folded along their length toward the aperture and appressed to the shell except at the keeled margin where they form rectangular processes that extend about 0.5 mm beyond the shell margin. The large, distally rounded processes overlap, forming a continuous periostracal fringe of uniform length at the shell periphery. Periostracal extensions on the growth lines extend basally but are short and erect. Nuclear whorls are white, postnuclear whorls yellow brown. The umbilicus is closed by a reflection of the peristome. The aperture is large, depressed-ovate, with an aperture-diameter/aperture-height ratio 0.53–0.66 (mean = 0.63).

The body color is uniform bright creamy-yellow in life, fading to creamy-white in specimens preserved in ethanol. The vas deferens narrows toward the junction with the slightly inflated head of the epiphallus (Figure 42). The epiphallus is approximately three times longer and one quarter of the diameter of the penis and does not bear a diverticulum. The penial retractor muscle is long, about two thirds the length of the epiphallus, originating from the diaphragm and inserting on the basal third of the epiphallus. The penis is short and robust with poorly defined pilasters in the apex (Figure 43). The atrium is short and narrow, expanding slightly towards the junction with the penis and the short vagina. The base of the spermathecal duct is massive, tapering slowly but remaining broad for more than one third of its length; the remainder is relatively narrow until the junction with the spherical spermatheca. The free oviduct is slightly coiled and narrow, joining the short vagina just above the atrium.

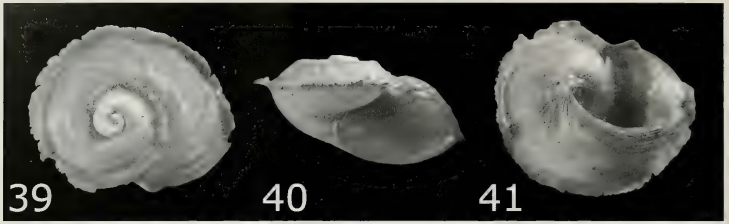
The central teeth of the radula (fifth row from left) are tricuspid, 9–10 μm wide and 14–15 μm long, roughly the same size and shape as the first lateral teeth (Figure 44). The mesocones of both the central and first lateral teeth are short, conical and erect, joining the rectangular basal plates nearly centrally and barely projecting beyond the plates' anterior margin. The ectocones are triagonal and short, only one third of the height of the mesocones, joining the posterior edge of the basal plates. The lateral teeth are asymmetrical; their endocones are slightly taller then their ectocones. The marginal teeth are dorsoventrally compressed, tricuspid to multicuspid, 8–10 μm wide and 10–12 μm long (Figure 45). The endocones of the marginal teeth are nearly the same height as the mesocones while the ectocones are much shorter, only one half to one third of their height and often divided into three cusps.

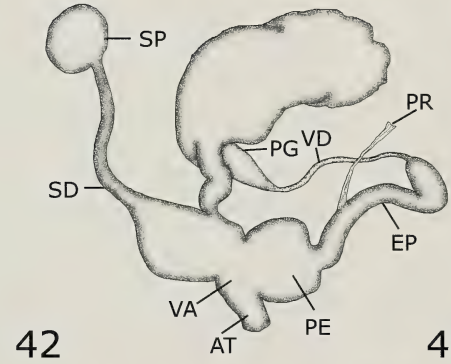
Type Material: Holotype: UF 308238, J. Slapcinsky, 6 April 2002; Paratypes: Papua New Guinea, Milne Bay Province: UF 299675 (2 specimens), UF 303594 (2 specimens), Wowow Mountain, W of Naura, 10°16.9′ S, 150°9.9′ E, 635 m altitude, J. Slapcinsky, 8 May 2002; UF 299673 (1 specimen), UF 303595 (1 specimen), 4 April 2002, UF 303598 (1 specimen), 27 February 2003, waterfall on Upalai Creek, 3 km WNW of Watunoa, 10°19.6′ S, 150°34.6′ E, 60 m altitude, J. Slapcinsky; UF 299670 (3 specimens), UF 299672 (6 specimens), 6 April 2002, UF 303596 (13 specimens), 7 March 2003, headwater of Goilayoli River at road crossing, 30 km ENE of Alotau, 10°18.7′ S, 150°37.3′ E, 275 m altitude, J. Slapcinsky; BPBM (4 specimens), MNHW 977 (4 specimens), PNGNM 004-104 (4 specimens), UF 303597 (45 specimens), small waterfall on Kinahidamadamana River near Budo Village, 10°17.1′ S, 150°26.7′ E, 125 m altitude, J. Slapcinsky, 4 March 2003.

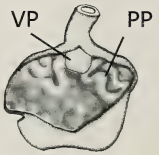
Type Locality: Papua New Guinea, Milne Bay Province, headwater of Goilayoli River at road crossing, 30 km ENE of Alotau, 10°18.7′ S, 150°37.3′ E, 275 m altitude.

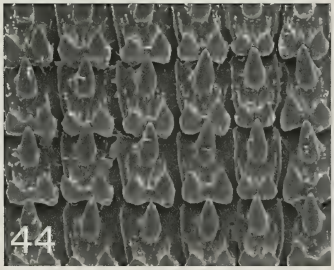
Habitat: This species was active during the day in native forest on rocks and logs with moss and algae, and on moist soil near streams. It was encountered in hilly terrain at relatively low altitudes for the genus, ranging from 60 to 635 meters.

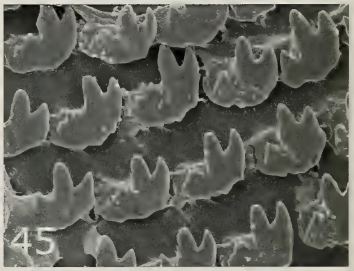
Etymology: This patronym honors Mr. Benjamin Yawi of Budo Village, Milne Bay Province, Papua New Guinea. He and his family located, arranged permission to visit, and helped to collect at many of the sites where this species was found.











Figures 39–45. *Paryphantopsis yawii.* **39–41.** Photographs of shell, Holotype UF 308238, diameter 6.5 mm. **42–43.** Camera lucida drawing of genitalia, UF 299672, maximum width 6.4 mm. **44–45.** Scanning electron micrograph of radula, UF 299672, field width of central and lateral teeth 63 μm, marginal teeth 48 μm.

Remarks: Peripheral keels are unusual among known *Paryphantopsis* species and are found only in *P. elegans, P. fultoni,* and to a lesser extent in *P. lebasii* and *P. lamelligera. Paryphantopsis yawii* is unlike all other species, except for *P. lebasii* and *P. fultoni,* in having large, rectangular periostracal extensions oriented parallel to the keeled shell margin. These peripheral extensions are all of equal length, unlike in *P. fultoni* and they overlap, forming a continuous periostracal fringe, unlike in *P. lebasii.*

DISCUSSION AND CONCLUSIONS

The family Charopidae was previously considered to be a minor component of the terrestrial molluscan fauna of New Guinea, with relatively few species and genera, and to lack the spectacular radiations exhibited by this and the related Endodontidae in the oceanic islands of the Pacific (Solem, 1983: 305). Ongoing surveys indicate that this is not the case; inadequate sampling, rather than low diversity, is the cause of the perceived low number of charopid species in New Guinea. Likewise, reports of low generic diversity of charopids in New Guinea are more likely the result of insufficient sampling and may reflect the paucity of anatomic material available to define generic units (Solem, 1970: 241). Despite the short duration and limited geographic scope of the current survey, six new species of *Paryphantopsis* are reported here, increasing the known diversity of the genus by almost 50%. In addition to *Paryphantopsis,* species belonging to several other charopid genera were also collected; these will be treated in later publications.

On the eastern terminus of the Papuan Peninsula, *Paryphantopsis* species that occur in close proximity or sympatry share unique shell, genital, and radular characters. For example, both species from the Mount Matawan area, *P. matawanensis* and *P. koragae,* have unusually short penial retractor muscles, long vaginas and angled apertural margins. Species in the uplands of the Cloudy Mountains, *P. ubwamensis* and *P. abstrusa,* are unusually tightly coiled and globose. The two lowland species, *P. lebasii* and *P. yawii,* share distally rounded rectangular periostracal processes and the unusual origin of their mesocones from the center of their basal plates. These unusual characters shared by different species in close proximity or sympatry suggest that *Paryphantopsis* species have speciated locally on a fine geographic scale; speciation in these cases is presumably facilitated by their poor dispersal ability. Because much of New Guinea remains under-explored, the true diversity of the islands' *Paryphantopsis,* other charopids, and land snails in general is almost certainly greatly underestimated.

The geographic distribution of the six *Paryphantopsis* species appears to be limited to particular mountain ranges on different terrains, despite the proximity of these mountains to each other (Figure 1). Three species, *P. matawanensis, P. koragae,* and *P. yawii* are restricted to the Owen Stanley Range, part of the Kutu Terrane, while three others, *P. abstrusa, P. lebasii,* and *P. ubwamensis,* are restricted to the Cloudy Mountains of the Port Moresby Terrane. These distinct suites of endemic species are consistent with the terrane-accretion hypothesis (Davis et al. 1997) proposed for the formation of the East Papua Composite Terrane and suggest that the low vagility and high diversity of charopids and other land snails may make them ideal to test hypotheses of terrain accretional history.

ACKNOWLEDGMENTS

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First record of *Akera* Müller, 1776, from the eastern Pacific, with the description of a new species

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ABSTRACT

The description of the new species *Akera julieae* is based on a complete specimen collected from southern California and three empty shells from Costa Rica. These specimens constitute the first record of *Akera* in the eastern Pacific. *Akera julieae* is distinguishable from the widespread Indo-Pacific species *Akera soluta* by its radular and jaw morphology; the rachidian teeth of *A. soluta* are more solid with larger cusps and flanking denticles, the mid-lateral teeth of *A. soluta* are denticulated, whereas in *A. julieae* they are smooth, and the outermost lateral teeth of *A. julieae* are proportionally more elongate and straighter than those of *A. soluta*; the jaws of *A. soluta* are well developed and composed of a number of rows of strong rodlets, whereas in *A. julieae* the jaws are more rudimentary with only five rows of fragile-looking rodlets. There are no consistent differences between these two species in gizzard plate and adult shell morphology, but the protoconch of *A. soluta* is slightly larger and more elongate. The western Atlantic species *Akera bayeri* is distinguishable from *A. julieae* by having a more elevated shell spire and stronger radular teeth with denticles on all lateral teeth.

INTRODUCTION

The opisthobranch family Akeridae Mazzarelli, 1891, includes opisthobranchs with an external, cylindrical shell into which the animal cannot retract completely. It contains the single genus *Akera* Müller, 1776, and only a few Recent valid species distributed throughout tropical and temperate regions. The type species, *Akera bullata* Müller, 1776, has been reported from the northeast Atlantic, from the Baltic shores of Denmark and Norway to the British Isles, continuing on to the Atlantic and Mediterranean costs of continental France and Spain (Thompson, 1976), Italy (Rinaldi, 1988), and the Canary Islands (Ortea et al., 2001).

In the Indo-Pacific, the widespread species *Akera soluta* (Gmelin, 1791) has been reported from South Africa and Mozambique to Australia, Marshall Islands, and the Philippines (Gosliner, 1987). Both *Akera bicincta* (Quoy and Gaimard, 1833), from Australia, and *Akera constricta* Kuroda 1947, from Japan, have been regarded as junior synonyms of *A. soluta*, see Wells and Bryce (1993) and Hamatani (2000) respectively. This expands the known range for *A. soluta*. Other nominal Indo-Pacific species, *Akera tumida* (A. Adams in Sowerby, 1850), *Akera tasmanica* Beddome, 1882, and *Akera aperta* Hedley, 1899, were all described from the southwestern Pacific, and are poorly known. They are likely synonyms of *A. soluta*, but because they were described based solely on shell morphology, their identities are unclear and in need of revision. In the western Atlantic, Olsson and McGinty (1951) reported for the first time a species of *Akera* from Florida under the name "Akera thompsoni." Because the animal was figured but not described, this species name is a *nomen nudum* in accordance with Article 13.1 of the International Code of Zoological Nomenclature (ICZN, 1999). The first available name for the western Atlantic *Akera* is *Akera bayeri* Ev. Marcus and Er. Marcus, 1967, which has been reported from the southwestern Caribbean Sea and Brazil (Ev. Marcus, 1970).

There are no Recent species of *Akera* known from the eastern Pacific. *Akera maga* Vokes, 1939, the only known species from this area, was described from the lower to middle Eocene, Domengine Formation, Fresno County, California (Vokes, 1939). Squires (2001) reported this species from the Llajas Formation (also lower to middle Eocene), Ventura County, California. In the present paper we describe the first occurrence of Recent *Akera* in the eastern Pacific based on a complete specimen collected in the Channel Islands, California and three shells from Guanacaste, Costa Rica.

MATERIALS AND METHODS

The specimen from California was collected as part of the Southern California Bight 1998 Regional Marine Monitoring Survey (Bight, 1998) conducted in the summer of 1998. Infaunal samples were taken with a 0.1 m^2 Van Veen grab sampler and screened through a 1 mm mesh. The sample was then placed in a relaxant solution of Epsom salts (magnesium sulfate heptahydrate—

Table 1. Comparative material examined in this study. The specimen marked with an asterisk (*) was collected alive and included soft parts.

Species	Locality	Date	Depth	Number
Akera soluta	Kii, Japan	—		LACM 153414*
	Uala Reef, Quezon, Philippines	May 1959	3–15 m	LACM 073035
	New Zealand	—	—	LACM 153415
	Hardwick Bay, South Australia	—	—	LACM 157942
	Hardwick Bay, South Australia	—	—	LACM 153416
	Hardwick Bay, South Australia	—	—	LACM 153417
	Phuket, Thailand	—	—	LACM 046386
Akera bullata	Finmark, Norway	—	—	LACM 153418

$MgSO_4 \cdot 7H_2O$) and freshwater for a minimum of 30 minutes. The sample was then fixed in 10% buffered formalin and preserved in 70% ethanol. The preserved whole animal was photographed using a digital camera mounted on a dissecting scope (Wild Epimarkroskop® M450).

The Costa Rican shells were collected during the Searcher 401 Expedition of the Natural History Museum of Los Angeles County.

Several additional specimens and shells belonging to other species of *Akera* were examined for comparison purposes. These specimens are listed in Table 1.

The shell is very fragile and could not be dissected intact from the specimens examined, which rendered the description below incomplete. Once the shell was removed, the internal organs were dissected and drawn using a Nikon SMZ 1000 microscope equipped with a drawing tube. The radula, jaws, and gizzard plates were dissected and photographed using a Hitachi S-3000N Scanning Electron Microscope (SEM). The apical region of the shell was separated from the rest of the shell and mounted for SEM photography.

SYSTEMATICS

Akeridae Mazzarelli, 1891
Akera Müller, 1776

Type Species: *Akera bullata* Müller, 1776, by monotypy.

Diagnosis: Shell external, fragile, translucent, cylindrical to slightly bulloid. Spire flattened to elevated with a partially embedded protoconch. Aperture equal to the length of the spire or slightly shorter. Thin periostracum forming a raised flange at the keel. Animal unable to retract fully into the shell, but can stretch over twice its length; with a posterior pallial tentacle. Parapodia extending laterally, meeting mid-dorsally over the shell. Radula with rachidian tooth having a median cusp and smaller denticles on either side. Rachidian tooth flanked by 21–52 lateral teeth. Gizzard with a number of irregular plates arranged in three tiers.

Akera julieae new species
(Figures 1–4)

Akera sp.—Behrens, 2004: 18, pl. 1D.

Holotype: LACM 3033, from type locality.

Paratypes: 3 shells, southeastern corner of Bahía Jobo, off sand beach west of Bahía de Salinas, Guanacaste Province, Costa Rica (11°02′22″ N, 85°45′16″ W), 14 Feb. 1972, 1.5–10.7 m depth (LACM 3034).

Type Locality: Southwestern corner of Santa Catalina Island, California, USA (33°18′24″ N, 118°22′05″ W), 24 Jul. 1998, 40.6 m depth, in gray colored silt and clay (LACM 3033).

External Morphology: The body is oval, 10 mm long in the preserved holotype. The cephalic shield is triangular, comprising about ¼ of the body length in the preserved specimen (Figures 1A, 2A). The parapodia are narrow and do not reach the midline of the body (Figures 1A–C, 2A). The gill is unipinnate, with 11 simple lamellae (Figure 2B). The color of the living animals is unknown; the preserved holotype is grayish white.

Shell Morphology: The shell is bullomorph, fragile, well-calcified (Figure 1). The protoconch is smooth, and only the outer whorl is visible externally (Figure 3C). Its maximum diameter is 200 μm. The whorls are separated by a deep, channelled suture, which is shallower on the apical whorls. The periphery of the whorls, near the apex, is angulated and forms a conspicuous keel, which divides the whorls into two parts (Figure 1D, 3C). The inner part has a characteristic pattern of strong, curved wrinkles. The whorls are attached to the preceding whorl just below the periphery of this whorl. The apical region is flattened and the external whorls overlap the most internal. The whorl sides are clearly curved, convex. The aperture is broad below and narrow above, where it extends into a deep sinus along the suture of the upper lip. There is a thin callus in the columella. The sculpture consists of numerous, low and thin spiral ribs and axial growth lines. The shells are covered with a thin brownish periostracum.

Anatomy: The buccal bulb is oval; it connects posteriorly to the long esophagus and the salivary glands (Fig-

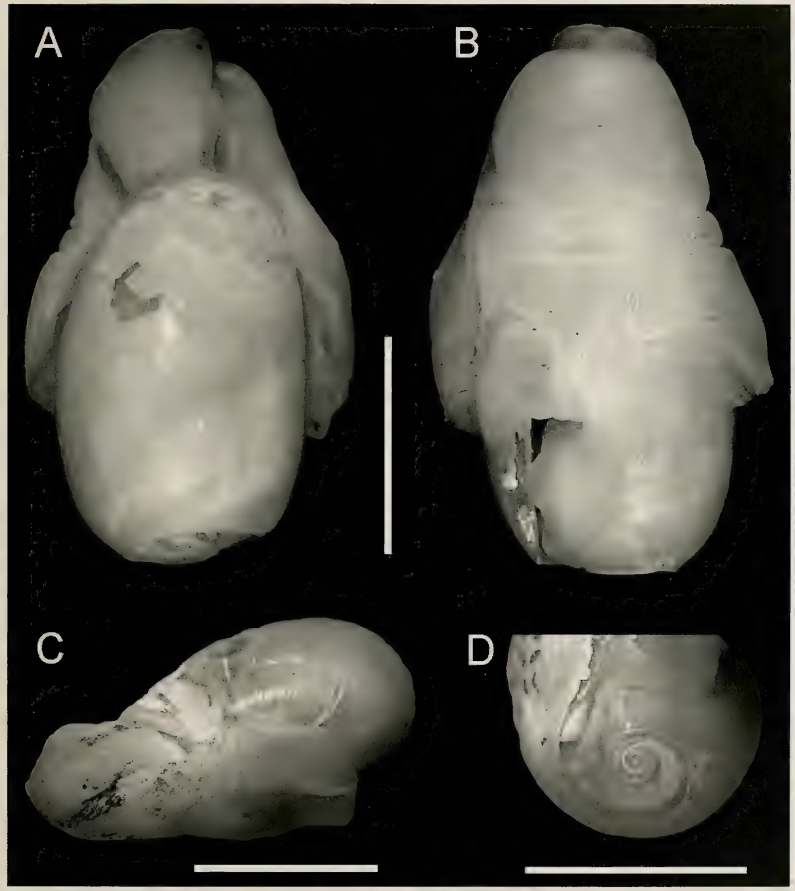

Figure 1. *Akera julieae* new species, photographs of the preserved holotype (LACM 3033). **A.** Dorsal view. Scale bar = 5 mm. **B.** Ventral view. Scale bar as in A. **C.** Lateral view. Scale bar = 5 mm. **D.** Apical view of the shell. Scale bar = 5 mm.

ure 2C). Two strong retractor muscles attach laterally to the buccal bulb. The radular formula is 19×23.1.23 in the holotype. The rachidian teeth are broad, with a triangular based, basally concave, and a pointed central cusp (Figure 4A). There are 3–5 denticles on each side of the cusp varying in shape and size. The two innermost teeth on each row have a long and narrow base and a conspicuously wider cusp bearing denticles on the inner

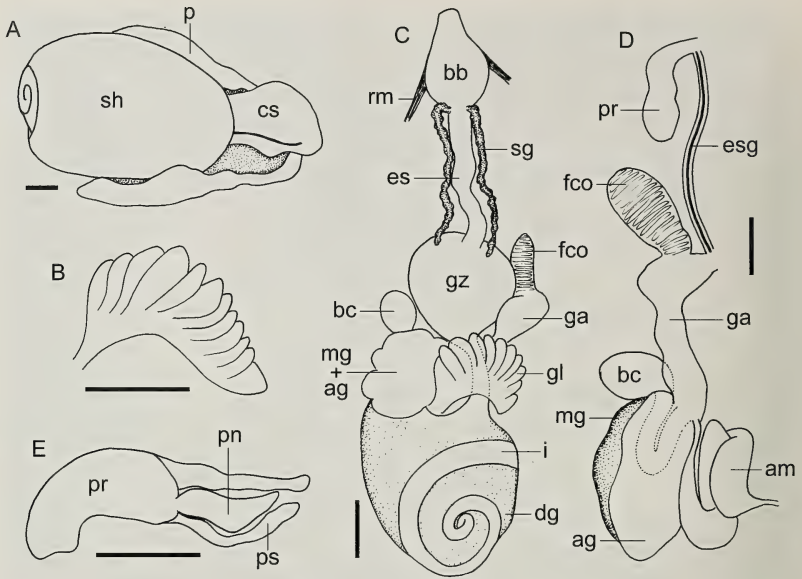

Figure 2. *Akera julieae* new species, drawings of the preserved holotype (LACM 3033). **A.** Dorsal view of the complete body. Scale bar = 1 mm. **B.** Detail of the gill. Scale bar = 1 mm. **C.** General view of the anatomy. Scale bar = 1 mm. **D.** General view of the reproductive system. Scale bar = 0.5 mm. **E.** Penis and prosate. Scale bar = 0.5 mm. Abbreviations: ag, albumen gland; am, ampulla; bb, buccal bulb; bc, bursa copulatrix; cs, cephalic shield; dg, digestive gland; es, esophagus; esg, external seminal groove; fco, female copulatory organ; ga, genital atrium; gl, gill; gz, gizzard; i, intestine; mg, mucous gland; pn, penis; pr, prostate; ps, penial sheath; rm, retractor muscle; sh, shell; sg, salivary gland; sr, seminal receptacle.

and outer sides. The rest of the lateral teeth are hook-shaped, with a long and narrow cusp and lack denticles (Figure 4B). In the outermost teeth the base is shorter and the cusp proportionally longer than in the mid-laterals (Figure 4C). The jaws are composed of 6 rows of simple, elongate rodlets (Figure 3B). The esophagus opens into a large muscular gizzard, which contains several gizzard plates. The gizzard plates vary in shape and size; they are irregular with angular edges (Figure 3A).

The reproductive system is monoaulic (Figure 2D). The ampulla is long and convoluted; it opens into the genital atrium at the same point where the albumen and mucous glands open. The bursa copulatrix is oval; it connects with the genital atrium through a wide and curved duct. The genital atrium is long and is connected to a complex female copulatory organ near the opening. From the gonopore an open seminal groove runs in anterior direction to the protrusible cephalic penis and the prostate. The penis is long and externally enclosed in a sheath (Figure 2E). The prostate is short and simple, and connects proximally to the penis.

Etymology: Dedicated to Julie Barwick, the daughter of the junior author.

DISCUSSION

Akera julieae has been included in *Akera* because of the presence of a fragile, cylindrical external shell, a flattened spire, and a partially embedded protoconch. The radula of this species has a single broad, triangular rachidian tooth, with a median cusp and smaller denticles on either side, as well as several hamate lateral teeth. The gizzard contains a number of irregular gizzard plates arranged in three tiers. All these characteristics are diagnostic of the genus *Akera* (see above).

This is the first record of *Akera* in the eastern Pacific. Behrens (2004) cited this species as *Akera* sp., based on

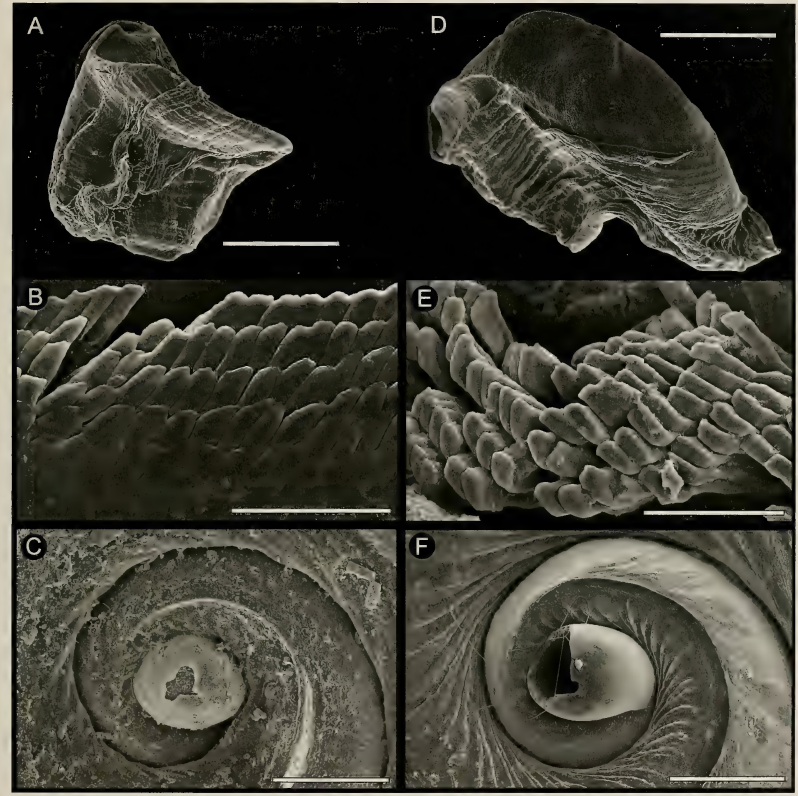

Figure 3. *Akera juliae* new species and *A. soluta* (Gmelin, 1791). **A–C.** *Akera julieae,* scanning electron micrographs of the preserved holotype (LACM 3033). **A.** Gizzard plate. Scale bar = 300 μm. **B.** Jaw. Scale bar = 50 μm. **C.** Protoconch. Scale bar = 200 μm. **D–E.** *Akera soluta* (Gmelin, 1791), scanning electron micrographs of a specimen from Japan (LACM 153414). **D.** Gizzard plate. Scale bar = 300 μm. **E.** Jaw. Scale bar = 50 μm. **F.** Protoconch. Scale bar = 200 μm.

the material here examined and information, photographs, and descriptions provided by the junior author. The description of the new species is mainly based on the holotype, collected from California, but the three empty shells collected from Costa Rica seem to belong to the same species. However, this needs to be verified when complete specimens from Costa Rica become available.

Akera julieae differs from other described species of the genus. Several shells and one specimen of the Indo-Pacific *Akera soluta* were examined for comparison (see Table 1) confirming the presence of several external and internal differences between these two species. For instance, the rachidian radular teeth of *A. soluta* are more solid with larger cusps and flanking denticles (Figure 4D). The three innermost lateral teeth have wide cusps

Figure 4. *Akera juliae* new species and *A. soluta* (Gmelin, 1791). **A–C.** *Akera julieae,* scanning electron micrographs of the radula of the holotype (LACM 3033). **A.** Rachidian and innermost lateral teeth. Scale bar = 50 μm. **B.** Mid-lateral teeth. Scale bar = 50 μm. **C.** Outermost lateral teeth. Scale bar = 50 μm. **D–F.** *Akera soluta,* scanning electron micrographs of the radula of a specimen from Japan (LACM 153414). **D.** Rachidian and innermost lateral teeth. Scale bar = 50 μm. **E.** Mid-lateral teeth. Scale bar = 50 μm. **F.** Outermost lateral teeth. Scale bar = 50 μm.

with denticles in *A. soluta,* whereas only the two innermost teeth of *A. julieae* have similar characteristics. The mid-lateral teeth in *A. soluta* also have denticles (Figure 4E), whereas they are smooth in *A. julieae.* The outermost lateral teeth of *A. julieae* are proportionally more elongate and straighter than those of *A. soluta* (Figure 4F). More importantly, the jaws of *A. soluta* are well developed and composed of a number of rows of strong rodlets (Figure 3E), whereas in *A. julieae* the jaws are more rudimentary with only 5 rows of fragile-looking rodlets. There are no consistent differences between the gizzard plates of *A. julieae* and *A. soluta* (Figures 3A, 3D). Externally, *A. soluta* has a slightly larger and more elongate protoconch. The adult shells of these two species are indistinguishable due to the morphological variability in *A. soluta.*

Akera bayeri is the only other species of *Akera* known from the Americas. The external morphology and anat-

omy of this species was described in detail by Marcus and Marcus (1967) and Marcus (1970). *Akera bayeri* differs from *A. julieae* in two important regards. The shell of *A. bayeri* has a more elevated spire and the radular teeth are stronger with denticles on all lateral teeth, whereas in *A. julieae* the lateral teeth are smooth.

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Description of *Calliotropis pulvinaris* new species (Gastropoda: Trochidae: Eucyclinae: Calliotropini) from West Madagascar

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ABSTRACT

Calliotropis pulvinaris new species is described from West Madagascar and compared with similar species in the trochid subfamily Eucyclinae, particularly with *C. patula* (Martens, 1904), *C. concavospira* (Schepman, 1908), *C. blacki* Marshall, 1979, and *C. vaillanti* (Fischer, 1882). The new species can be separated from these by a rather depressed spire, a rounded periphery, tumid whorls bearing four spiral cords of which nodules decrease in size and increase in number from adapical cord to abapical cord, and five spiral cords on the base.

INTRODUCTION

The malacofauna of this area remains poorly known, despite earlier surveys (1971–1973) by ORSTOM (Office de la Recherche Scientifique et Technique Outre-Mer, now IRD: Institut de Recherche pour le Développement) on the continental slope of Madagascar (Crosnier and Jouannic, 1973). Independently of the inherent economic interest, this endeavor yielded abundant zoological material, more particularly mollusks now deposited at the MNHN (Muséum national d'Histoire naturelle, Paris).

Commercial fishing boats have trawled for deep-water shrimp off Madagascar. The commercial dredging off West Madagascar from these last years brought various specimens of trochid species, some of them described in the past (Watson, 1886; Martens and Thiele, 1904; Thiele, 1925; Barnard, 1963), others recently named as new species (Vilvens, 2001 and 2002). Two years ago, Guido T. Poppe entrusted me with trochid shells collected in deep water. These shells, originally labeled as *Calliotropis patula* (Martens, 1904), are conspecific with material trawled by French expeditions and deposited at MNHN in the 1970s. Closer examination and comparison with the type of the supposed species leads me to conclude that all these shells belong to an unnamed species that is described here as new.

Text abbreviations used are: IRSNB: Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium; MNHN: Muséum national d'Histoire naturelle, Paris, France; NMNZ: Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; ZMA: Zoölogisch Museum, Amsterdam, The Netherlands; ZMB: Zoologisches Museum of Berlin, Germany; P1, P2, P3, P4: primary cords (P1 is the most adapical); stn: station; dd: no live specimens present in sample.

I follow below the classification of Hickman and McLean (Hickman and McLean, 1990) at the suprageneric level.

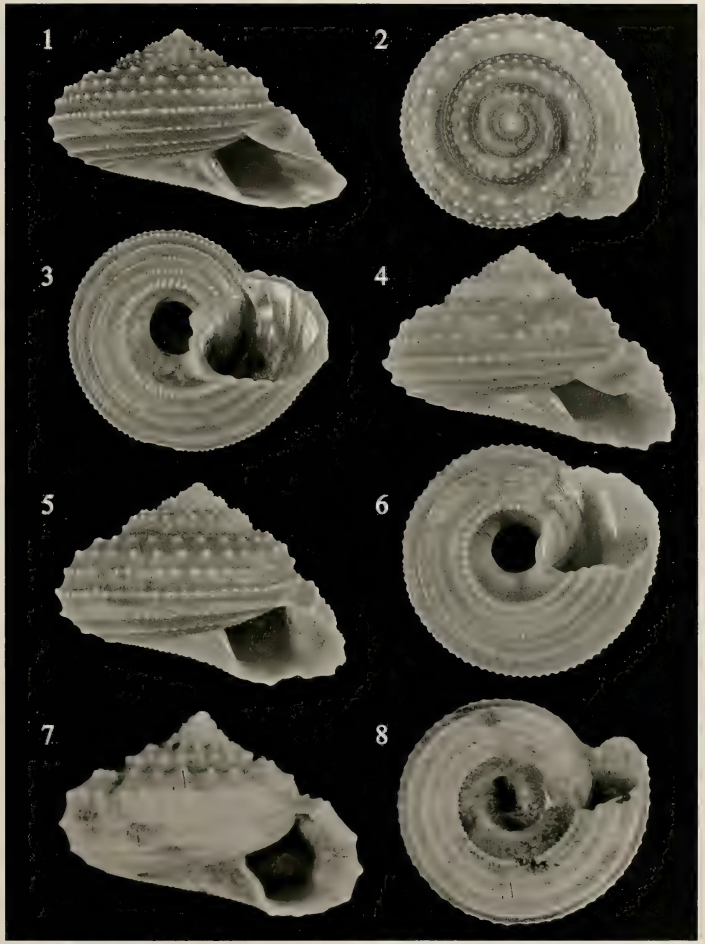
SYSTEMATICS

Family Trochidae Rafinesque, 1815
Subfamily Eucyclinae Koken, 1897
Tribe Calliotropini Hickman and McLean, 1990
Genus *Calliotropis* Seguenza, 1903

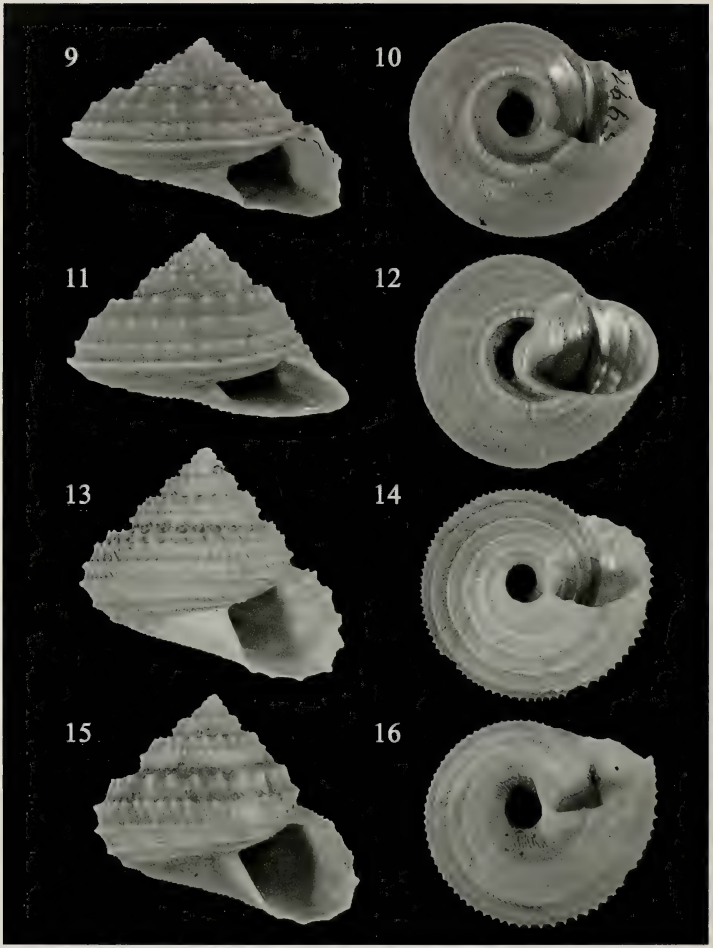
Type Species: *Trochus ottoi* Philippi, 1844, Pliocene–Pleistocene, Italy; by original designation.

Calliotropis pulvinaris new species
(Figures 1–6)

Description: Shell rather long for genus (height up to 18.3 mm, width up to 29.0 mm), rather depressed, rather thin, cyrtoconoidal; spire rather low, height 0.6–0.7×width, height 2.3–4.5×aperture height; umbilicus deep and large. Protoconch about 300 μm wide, with about 1 whorl, partially damaged on available specimens, remaining part smooth. Teleoconch of up to seven convex whorls, bearing four spiral granular cords and prosocline threads; nodules from cords produced by intersections with axial folds on four first whorls; additional axial threads not connecting nodules on last whorls. Suture visible, impressed, not canaliculated. First teleoconch whorl convex, sculptured by about 18–20 prosocline smooth riblets, interspace between riblets twice as wide as riblets; primary spiral cords P2 and P3 appearing almost immediately, evenly spaced, similar in size and shape, bearing rounded nodules produced by intersection with axial riblets. On second whorl, P2 and P3 stronger, P1 appearing at end of whorl, close to P2. On third whorl, nodules of P1 and P2 becoming sharp, with weak-



Figures 1–8. *Calliotropis* species. **1–6.** *Calliotropis pulvinaris* new species. **1–3.** Holotype MNHN, northwestern Madagascar, 18.1×29.0 mm. **4.** Paratype IRSNB, West Madagascar, 18.1×26.6 mm. **5–6.** Paratype, collection C. Vilvens, West Madagascar, 18.3×25.4 mm. **7–8.** *C. concavospira* (Schepman, 1908), syntype ZMA, Indonesia, 6.0×8.7 mm.



Figures 9–16. *Calliotropis* species. **9–12.** *Calliotropis patula* (Martens, 1904). **9–10.** Syntype ZMB 55919, between Zanzibar and Brawa, 16.2×25.1 mm. **11–12.** Syntype ZMB 109933, Somaly, 19.0×27.2 mm. **13–14.** *C. blacki* Marshall, 1979, holotype NMNZ M226932, Raoul Island, Kermadec group, 11.3×13.0 mm. **15–16.** *C. vaillanti* (Fischer, 1882), MNHN, Azores Islands, 10.6×12.2 mm.

Table 1. *Calliotropis pulvinaris*. Shells measurements in mm for all types cited and type material (n=8). H: height; W: width; HA: aperature height; TW: number of teleoconch whorls.

	Measurement					
	TW	H	W	HA	H/W	H/HA
Range	5.75–7.00	15.4–18.3	21.8–29.0	4.00–6.90	0.60–0.70	2.30–4.50
Mean	6.69	17.11	24.7	5.71	0.69	3.10
Standard deviation	0.41	0.97	2.13	0.93	0.03	0.70

ly adapically oriented tip; P4 partially covered by succeeding whorl, with nodules smaller and more numerous than ones on other cords. From fourth whorl on nodules on cords decrease in size and sharpness, and increase in number from P1 to P4; cords evenly distributed on whorl; axial threads in area between cords remain thin, distance between threads similar to threads width. On last whorl, P4 peripheral; no secondary spiral cords; periphery rounded.

Aperture almost circular, forming angle at junction of inner and outer lips; this angle almost rounded and outer lip slightly flared in fully mature specimens; inner lip flanged in a curved arc projecting weakly over umbilicus; parietal lip forming thin, transparent glaze. Columella slightly curved, without tooth, abapical part prosocline. Base moderately convex, with 5 granular spiral cords, innermost one stronger than others and bordering umbilicus; interspace between cords twice as wide as cords, smaller for two innermost cords on young adult specimens; very fine axial lamellate threads between cords, poorly visible. Umbilicus wide, funnel shaped, diameter about 35% of shell diameter, with very fine crowded axial lamellae and no spiral cord within. Color of protoconch and teleoconch pinkish white, with no maculations; first two whorls somewhat brownish.

Type Locality: West Madagascar, 22°17.0′ S, 43°02.2′ E, 640–660 m, Indian Ocean.

Type Material: Holotype MNHN unnumbered (dd), Chalutages *Vauban,* stn. CH 112, coll. A. Crosnier, from type locality, 18.1×29.0 mm; Paratype 1 MNHN unnumbered (dd), 12°50′S, 48°09′E, 580–585 m, northwestern Madagascar, coll. A. Crosnier; Paratypes 2 MNHN (dd), 1 IRSNB (IGnr 30 185) (dd), 1 ZMB (Moll. 108.519) (dd), 1 G. T. Poppe collection (dd), 1 C.Vilvens collection (dd), all from West Madagascar, off Mahajanga (formerly Majunga), commercial trawlers said to be from 800 m.

Etymology: Of a cushion (Latin); with reference to the soft and oval form of the shell, without angulations.

Remarks: *Calliotropis pulvinaris* new species is similar to *C. patula* (Martens, 1904) (Figures 9–12) from East Africa (off Somalia and Zanzibar, 977–1019 m), but this species differs from the new species by having a subangulated periphery, less tumid whorls, four spiral cords on base (instead of 5) and also by the nodules of P1 and P2 that become bigger than those of P3 much later (4th whorl).

The new species weakly resembles *C. concavospira* (Schepman, 1908) (Figures 7–8) from Indonesia (also deep water from 835 to 883 m), but this smaller species has only three cords on the whorls and these whorls are more angulated.

Calliotropis pulvinaris new species may also be compared to *C. blacki* Marshall, 1979 (Figures 13–14), from Kermadec Islands, but this Indo-Pacific species is smaller for a similar number of whorls, has a more elevated spire and only four spiral cords on the base.

The new species is also superficially similar to *C. vaillanti* (Fischer, 1882) (Figures 15–16) and *C. ambigua* (Dautzenberg and Fischer, 1896), both from eastern Atlantic, and to *C. actinophora* (Dall, 1890) from western Atlantic, but these three species have a more elevated spire, only 3 spiral cords on the whorls and only four spiral cords on the base.

ACKNOWLEDGMENTS

I would like to express my warm thanks to P. Bouchet (Muséum national d'Histoire naturelle, Paris) for access to the malacological resources of the MNHN, and V. Héros (MNHN) for her help in my search for scientific papers. Also, I am especially grateful to J. L. Van Goethem (Institut royal des Sciences naturelles de Belgique) for his constant help, particularly with loan of types. I also would like to thank F. Koehler (Museum für Naturkünde, formerly Zoologisches Museum, Berlin), B. A. Marshall (Museum of New Zealand Te Papa Tongarewa, Wellington) and R. Moolenbeek (Zoölogisch Museum, Amsterdam) for the loan of types from their institution. Finally, I highly appreciate the judicious advice of R. Houart.

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Notice

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The Curatorship, established originally in accordance with the wishes of the late Dr. R. Tucker Abbott, Founding Director of the Shell Museum, is awarded annually to enable malacologists to visit the museum for a period of one week. Abbott Fellows will be expected, by performing collection-based research, to assist with the curation of portions of the Museum's collection and to provide one evening talk for the general public. The Museum collection consists of marine, freshwater, and terrestrial specimens. A large percentage of our holdings have been catalogued through a computerized database management system. A substantial portion of the time will be available for research in the collection, but field work in southwest Florida can be arranged. The R. T. Abbott Visiting Curatorship is accompanied by a stipend of $1,500.

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Dr. José H. Leal, Director
The Bailey-Matthews Shell Museum
P.O. Box 1580
Sanibel, FL 33957
jleal@shellmuseum.org

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CONTENTS

Guido Pastorino — A revision of the genus *Trophon* Montfort, 1810 (Gastropoda: Muricidae) from southern South America 55

Alvar Carranza
Walter Norbis — Latitudinal trends in shell characters of the neogastropod *Olivancillaria urceus* (Gastropoda: Olividae) in the temperate southwestern Atlantic Ocean 83

Errata 90

A revision of the genus *Trophon* Montfort, 1810 (Gastropoda: Muricidae) from southern South America

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ABSTRACT

The genus *Trophon* from southern South America is revised and restricted to ten valid species from among the 36 nominal species still currently used. In addition, a new species, *Trophon parodizi* from Patagonian waters, is described. Adult specimens of the new taxon are illustrated, described and compared with other living species of the same genus and similar geographic distribution. Redescription and re-illustration of types, based on material from several institutions around the world are provided for *Trophon geversianus* (Pallas, 1774), *T. plicatus* (Lightfoot, 1786), *T. patagonicus* (d'Orbigny, 1839), *T. acanthodes* Watson, 1882, *T. pelseneeri* Smith, 1915, *T. amettei* Carcelles, 1946, *T. clenchi* (Carcelles, 1953), *T. wilhelmensis* Ramirez-Bohme, 1981, and *T. bahamondei* McLean and Andrade, 1982. In addition, "*Trophon*" *malvinarum* Strebel, 1908, assigned to *genera incerta*, is also redescribed and illustrated.

INTRODUCTION

Among many groups of marine gastropods from South American waters in need of a modern comprehensive revision, the high diversity and abundance exhibited by the muricid genus *Trophon* Montfort, 1810, renders it particularly interesting. Early collections include a large and varied array of specimens obtained by 19th century expeditions from shallow waters of a vast area including more than 5,000 km of coast in Argentina. A taxonomic revision of these gastropods revealed that a large number of names should be placed in synonymy. The taxonomy and nomenclature thus clarified is sure to improve the usefulness of this genus and its species as tools for biogeographic and evolutionary interpretations, without forgetting that clear specific delimitation is crucial to other uses such as the commercial exploitation of the type species (*Trophon geversianus*) in southern Chile.

The subfamily Trophoninae is one of the most conspicuous groups of marine gastropods living presently around the southern tip of South America. The southern origin of the group seems to be beyond doubt, as discussed by Griffin and Pastorino (2005), when revising the numerous extinct species appearing in the fossil record since the late Oligocene.

This article constitutes a review of all living species of *Trophon* from both coasts of southern South America. The study involves only those taxa living in environments associated with the continental shelf. Accordingly, *T. mucrone* Houart, 1991, from 1500–1575 m off Brazil and the subantarctic *T. veronicae* Pastorino, 1999, are not considered herein. These two deep-water species seem to belong in a different group according to data available on the radula, protoconch, and penis of *T. veronicae*. Such anatomical data remain unknown for *T. mucrone*. In addition, *T. ohlini* Strebel, 1904, with a distinct protoconch and radula, different from those of other Patagonian species and resembling the boreal *Boreotrophon truncatus*, will be the subject of a future paper. Finally, *T. triacanthus* Castellanos et al., 1987, recently described under *Trophon*, is also considered as belonging to a different genus—possibly *Apyxistus*—according to several differences in protoconch and shell morphology.

Houart (2003) recently described three new species under the genus *Trophon* sensu lato from dredgings more than 1000 m in depth. No radular, anatomical, or protoconch information is included in the descriptions. However, enough differences can be observed in the shells that, as mentioned by Houart himself, a new genus may be granted for these species. A similar situation is true for "*Trophon*" *malvinarum*; however, as there are no accurate illustrations or recent descriptions of this species I decided to include it in this work as belonging to an indeterminate genus.

For each of the species considered herein, adult specimens, operculum, gross anatomy, radula, protoconch, and ultrastructure of the shell are described whenever enough material was available. This work is part of a complete revision of the genus including all species from South America and Antarctica.

MATERIALS AND METHODS

All the material examined is housed in the collections of the Museo Argentino de Ciencias Naturales "Bernardino

Rivadavia", Buenos Aires (MACN-In); Museo de La Plata, La Plata (MLP); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and American Museum of Natural History, New York (AMNH). Part of the type material is housed in the following museums: The Natural History Museum, London, (BMNH); Zoologisches Institut und Zoologisches Museum der Universität Hamburg, (ZMH); Swedish Museum of Natural History, Stockholm, (NHRM); Museum national d'Histoire naturelle, Paris (MNHN); Museo Nacional de Historia Natural, Santiago, Chile (MNHNS); Museo Nacional de Historia Natural, Montevideo, Uruguay (MNHNM); Academy of Natural Sciences of Philadelphia (ANSP) and Los Angeles County Museum of Natural History (LACM). Finally, several historical specimens from the Auckland Institute and Museum, New Zealand (AK) were examined for comparative purposes. Material from the USNM originates from the United States Antarctic Program (USAP) and was mostly collected by two ships: R/V Hero and R/V Eltanin. Material collected by the Uruguayan ship R/V Aldebaran is also included.

Dissections were performed on ethanol-preserved specimens for study of gross anatomy, with emphasis on the morphology of the anterior alimentary system, and the pallial portions of the male and female reproductive systems. Radulae were prepared according to the method described by Solem (1972) and observed using a LEO 440 scanning electron microscope (SEM) at the USNM and a Philips XL 30 at MACN. Radular terminology follows Kool (1993, fig. 6B). Shell ultrastructure data were procured from freshly fractured colabral sections taken from the central portion of the lip on the last whorl of two individuals per taxon, whenever sufficient material was available.

Photographs were taken using a digital scanning camera. Several images were scanned from black and white 35 mm negatives using a slide scanner. All images were digitally processed.

For the convenience of the reader in the Additional Material Examined sections, "D" means that the specimens were collected dead and "A" means alive.

SYSTEMATICS

Class Gastropoda Cuvier, 1791
Subclass Ortogastropoda Ponder and Lindberg, 1996
Superorder Caenogastropoda Cox, 1959
Order Sorbeoconcha Ponder and Lindberg, 1996
Infraorder Neogastropoda Wenz, 1938
Family Muricidae da Costa, 1776
Subfamily Trophoninae Cossmann, 1903
Genus *Trophon* Montfort, 1810

Type Species: *Murex magellanicus* Gmelin, 1791 (=*Buccinum geversianus* Pallas, 1774) by original designation. *Polyplex* Perry, 1811 (type species *Polyplex bulbosa* Perry, 1811 =*Buccinum geversianum* Pallas, 1774) and *Muricidea* Swainson, 1840 (type species *Murex magellanicus* Chemnitz, 1780 (*nomen nudum*) =*Murex magellanicus* Gmelin, 1791 =*Buccinum geversianum* Pallas, 1774) are synonyms.

Description: Shells variable in size, ranging from about 1 to more than 10 centimeters high, fusiform, subquadrate to elongate. Protoconch paucispiral, with 2 to 2½ asymmetrical, smooth, slightly globose, and regularly convex whorls. Spire of about 4 whorls, equal or slightly shorter than aperture height, never higher. Subsutural ramp generally present, variously developed and slightly inclined posteriorly, defining a conspicuous keel. Axial sculpture variable, from weak growth lines to strong lamellae—in some instances even growing over the subsutural ramp; axial sculpture generally better developed than spiral sculpture. Lamellae along keel sometimes growing into fairly strong, always open, spines, which may even curve backwards. Spiral ornamentation variably developed; sometimes missing, but generally consisting of slightly rounded and equally developed cords, wider than interspaces and sometimes accompanied by weaker secondary intercalated ones. Spiral ornamentation usually restricted to surface abapical to keel, while missing along subsutural ramp and in some cases only present in the earliest whorls. Aperture subovoid; outer lip sharp, sometimes slightly reflected, but always smooth throughout. Siphonal canal always present and open, although variably developed in length, sometimes curved. Umbilicus variable, usually open, wide, although in some species totally absent or represented by a chink.

Shell ultrastructure arranged invariably in 2 layers: innermost layer of crossed lamellar aragonite, outer layer of amorphous calcite. Relative thickness of both layers variable according to species or—within a given species—latitude at which the population lives.

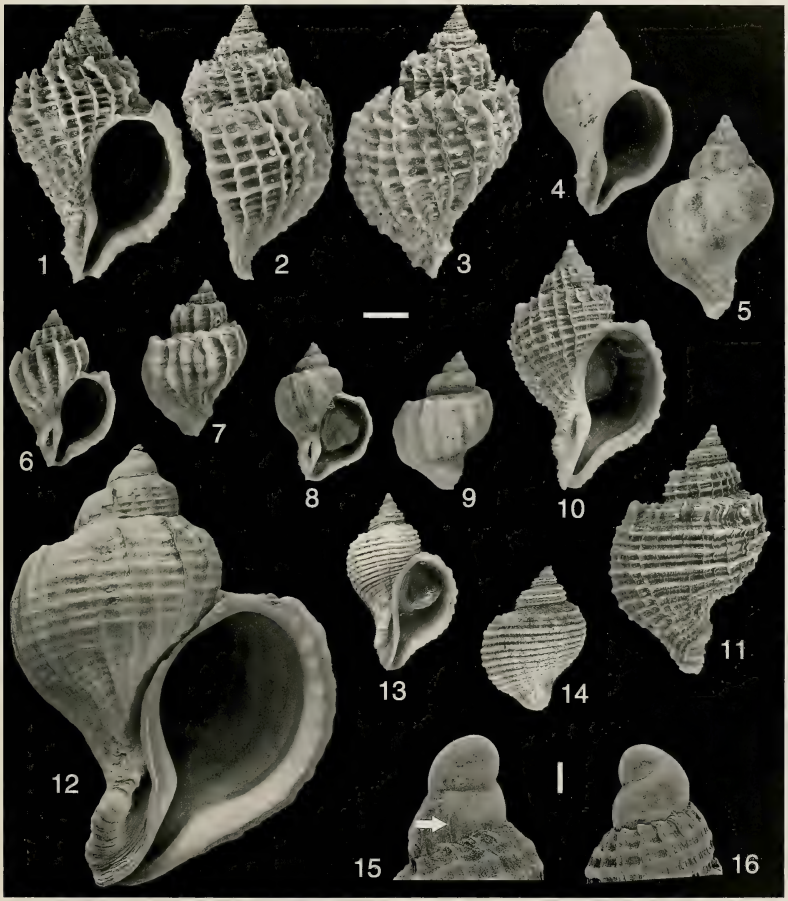
Radulae rachiglossate, rachidian teeth with 3 median cusps, the central one the larger and the lateral ones with a denticle, sometimes obsolete but always present, attached to the interior margin (never free). Rachidian base always sinuous and with the base offset under the proximal tooth. Marginal cusps always single, never bifid. Lateral teeth always thin, with the attachment area also thin. Operculum circular or suboval tear-shaped, attachment area with horseshoe shaped scars.

Accessory salivary glands always developed, tubular, single or coiled and unfilled. Esophagus with a loop running along the left side of the gland of Leiblein; esophageal glands externally invisible.

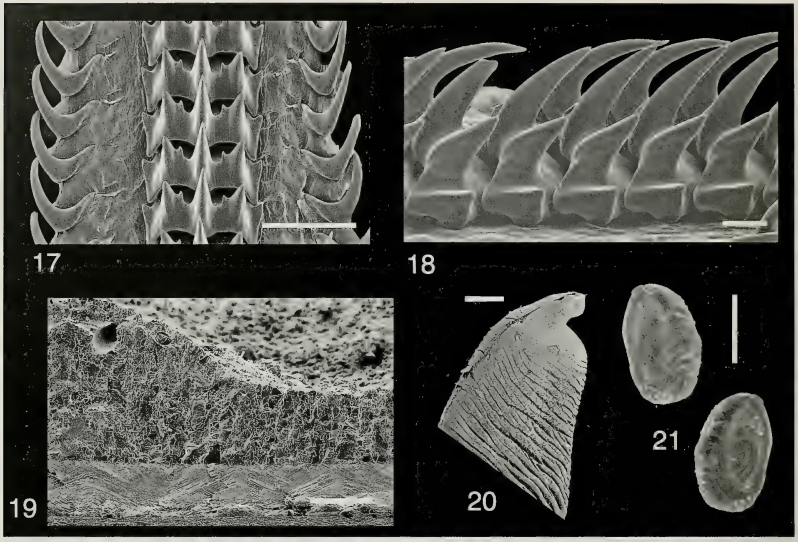
Egg-capsules always erect, never lenticular, usually with nurse eggs.

Trophon geversianus (Pallas, 1774)
(Figures 1–21)

"Purpurschnecken" Knorr, 1769: 47, pl. 30, fig. 2.
"Buccin feuilleté" Knorr, 1770: 53, pl. 30, fig. 2.
Buccinum geversianum Pallas, 1774: 33, pl. 3, figs. 1, 2.
Buccinum foliaceum multifariam frondosum Chemnitz, 1780: 130, pl. 139, fig. 1297 [non-binominal, rejected by Opinion 184 (ICZN, 1944) [Lectotype of *Murex magellanicus* Gmelin, 1791 (Beu, 1978)].



Figures 1–16. *Trophon geversianus* (Pallas, 1774). **1–3.** MACN-In 36036, Punta Cavendish, Puerto Deseado, Santa Cruz province in 5 m. **4–5.** MACN-In 36042, Cueva del Indio, Puerto Deseado. **6–9.** MACN-In 36041, Sierra Grande, Río Negro province, in tide pools. **10–11.** MACN-In 36037, Punta Peñas, San Julián, Santa Cruz Province in 2 m. **12.** MACN-In 36043, Bahia Almanza, Puerto Harberton, Tierra del Fuego, in 3 m. **13–14.** MACN-In 36038, both specimens from Playa La Mina, San Julián, Santa Cruz Province intertidal. Scale bar for all shells = 1 cm. **15–16.** Two views of protoconch, arrow head the transition to teleoconch. Scale bar = 500 μm.



Figures 17–21. *Trophon geversianus* (Pallas, 1774). **17.** Radula, frontal view. Scale bar = 100 μm. **18.** Lateral view of the same radula. Scale bar = 30 μm. **19.** Ultrastructure of the shell. Scale bar = 100 μm. **20.** Penis, critical-point dried. Scale bar = 800 μm. **21.** two views of the operculum. Scale bar = 1 cm.

Buccinum fimbriatum Martyn, 1784: fig. 6.
Murex magellanicus Gmelin, 1791: 3548 *partim* (var. β excl.); d'Orbigny 1841: 451; Wood, 1828: 127, pl. 26, fig. 90; Hanley, 1856: 132, pl. 26, fig. 90.
Neptunea foliacea Röding, 1798: 116.
?*Murex ventricosus* Molina, 1810: 178.
Polyplex bulbosa Perry, 1811: pl. 9, fig. 5.
Murex foliatus Schumacher, 1817: 215, sensu Vokes 1971.
Fusus magellanicus Lamarck. Gray, 1839: 118.
?*Murex varians* d'Orbigny, 1839: pl. 42, figs. 4–7; d'Orbigny, 1841:452.
T. geversianus Pallas.—Montfort, 1810: 483, fig.; H. and A. Adams, 1853: 77, pl. 8, fig. 3 c.; Tapparone-Canefri, 1874: 15; Kobelt, 1878: 205, pl. 72, fig. 1–3; pl. 73, fig. 1; Sowerby II, 1880: pl. 404, figs. 7,8; Tryon, 1880: 144, pl. 32, figs. 337–340, 343–347; pl. 70, figs. 433; Watson, 1886: 164; Rochebrune and Mabille, 1889: H.53; Strebel, 1904: 173, pl. 4, figs. 11–23; pl. 5, figs. 24–42; pl. 6, figs. 43–52; Lamy, 1906: 3; Ihering, 1907: 404; Melvill and Standen, 1907: 106; Strebel, 1908: 37, pl. 6, figs. 94 a, b.; Carcelles, 1946: 60, figs. 1–5; 1946: 69, figs. 6a,b; 7a,b,c,d; 8; Powell, 1951: 151, fig. L, 81; N, 107; Castellanos, 1970: 76, pl. 5 fig. 2; Dell, 1971: 210; Harasewych, 1984: 13, figs. 1–3, 19–25; Vokes, 1991: 7, fig.; 1992: 3, figs 1c, d; 3c, d; Kool, 1993: 47, figs. 9–14, 30–31; Castellanos and Landoni, 1993: 3, pl. 1 figs. 1–15, 18–21.
Fusus intermedius Hupé in Gay, 1854: 166, pl. 4, fig. 6, *non* Cristofori and Jan, 1832 *nomen nudum*; *nec* A. J. Michelotti, 1846 *nomen nudum*; *nec* G. Michelotti, 1847; Rochebrune and Mabille. 1889: H.53.
F. geversianus Pallas.—Hupé in Gay, 1854: 167; Gould, 1861: pl. 16, fig. 277 a, b.
Trophon geversianus var. *calva* Kobelt, 1878: 305, pl. 75; fig. 1.
T. geversianus var. *tirata* Kobelt, 1878: 305, pl. 76, fig. 1, 2.
T. philippianus Dunker in Kobelt, 1878: 277, pl. 72, figs. 4, 5; Melvill and Standen, 1907: 107; Powell, 1951: 152.
T. philippinarum Dunker. Sowerby II, 1880: pl. 405, fig. 21.
?*T. varians* (d'Orb.).—Carcelles, 1943: 431, figs. 1, 2, 3, 6, 7; Castellanos, 1970: 75, pl. 5, fig. 3, 4; Vokes, 1992: 3 fig. 4c.
T. plicatus (Lightfoot).—Calvo, 1987: 135, fig. 99.
Trophon sp. Vokes 1991: 9, figs. 1–13.

Description: Shell large (up to 100 mm) and extremely variable, fusiform, subquadrate profile, chalky, whitish; protoconch of 2 whorls, smooth, cylindrical, slightly globose, slightly asymmetrical; teleoconch of 4 shouldered whorls, spire less than ⅓ of total shell height. Spire angle about 50°; suture impressed; subsutural shelf straight, aperture ovoid, interior glossy pinkish; anterior siphonal canal moderately long (half the height of aperture); umbilicus closed or deep, some specimens with a pseu-

doumbilical chink; outer lip rounded, with reflected edges; inner lip curved, adpressed.

Axial ornamentation of irregular, low lamellose varices on first whorls, becoming 8–10 well-defined lamellae on last ones. Lamellae growing across entire whorl, attached to the shell, sometimes curving adaxially. Lamellae ending in shallow peripheral spine, in some specimens growing adapically.

Spiral ornamentation of about 15 cords beginning at periphery of whorls. Smooth specimens common in intertidal pools and mytilid banks. Coloration varying from creamy white to dark brown. Growth lines regularly spaced, present throughout shell. Geographic variation conspicuous from north to south and from intertidal to infralittoral specimens, expressed as a series of smooth to profusely ornamented specimens according to area of collection.

Shell ultrastructure composed of two layers; innermost layer (50% shell thickness) of colabrally aligned crossed lamellar aragonite, outer layer (50% shell thickness) with amorphous calcite.

Operculum oval, brownish, with terminal nucleus. External surface covered by concentric, irregular, growth lines. Inner surface attachment area with 3 horseshoe-shaped scars, thick glazed rim present in all specimens.

Anatomical and radular characters as described by Harasewych (1984) and Kool (1993).

Type Material: The type material upon which Pallas (1774) based *Buccinum geversianum* could not be located. It could not be found at the Zoological Institute of the Russian Academy of Sciences (ZIL) St. Petersburg, where most of the material studied by that author is housed (B. Sirenko, pers. comm.).

Additional Material Examined: 53°39′ S, 70°55.5′ W, 5 A, R/V Hero Cruise 702, Sta. 466, 25 April 1970, 20 m (USNM 901605); 53°39′ S, 70°55.5′ W, 6 A, R/V Hero Cruise 702, Sta. 473, 26 April 1970, 15–18 m (USNM 901609); 53°30′48″ S, 70°50′33″ W, 4 A, R/V Hero Cruise 692, Sta. 69-11, 24 April 1969, intertidal, (USNM 901604); 53°24.8′ S, 69°39.2′ W, 1 D, R/V Hero Cruise 702, Sta. 481, 27 April 1970, 18 m, (USNM 901605); 53°17′ S, 68°13′ W, 1 A, R/V Hero Cruise 712, Sta. 71-2-6, 21 April 1971, 1 m, (USNM 886739); 53°51′32″ S, 70°25′52″ W, 1 A, R/V Hero Cruise 692, Sta. 69-22, 13 May 1969, 2–3 m (USNM 886187); 53°37.9′ S, 70°14′ W, 1 D, R/V Hero Cruise 702, Sta. 486, 28 April 1970, 292–296 m (USNM 901602); 54°59′ S, 64°53′ W, 1 D, R/V Eltanin Cruise 11, Sta. 970, 11 February 1964, 586–641 m (USNM 870515); 53°48.7′ S, 70°24.1′ W, 1 D, R/V Hero Cruise702, Sta. 489, 29 April 1970, 13–18 m (USNM 901601); 54°27′ S, 66°12′ W, 2 D, R/V Eltanin Cruise 6, Sta. 453, 21 January 1963, 31 m (USNM 901600); 53°26′ S, 68°35′ W, 6 A, R/V Eltanin Cruise 21, Sta. 297, 12 January 1966, 0 m (USNM 901607); 53°35′ S, 70°50′ W, 1 D, 1 A, R/V Eltanin Cruise 21, Sta. 292, 8 January 1966, 0 m (USNM 901606); 53°17′ S, 68°13′ W, 3 D, R/V Eltanin Cruise 712, Sta. 71-2-6, 21 April 1971, 0–1 m (USNM 901608); Puerto Basil Hall, Isla de los Estados, 10 A, 21 May 1971, 0–1 m (MLP 4243); Buen Suceso Bay, Tierra del Fuego, 4 A, 23 October 1941 (MLP 27218); San Julián, Punta Peñas, 6 A, 1 March 1924 (MLP 526 *partim*); Puerto Lobos, Chubut, 12 A, 2 February 1938 (MLP 2021); Puerto Golondrina, Ushuaia, 9 A, January 1962 (MLP 27201); Puerto Pirámides, Chubut, 1 A (MLP 4715); San Julián, 8 A (MLP 1583); Puerto Hoppner, Isla de los Estados, 7 A (MACN-In 22547); Punta Cavendish, Puerto Deseado, 7 A, 6 February 1961 (MACN-In 26171); Punta Cavendish, Puerto Deseado, Santa Cruz province, 5 m (MACN-In 36036); Chubut, 6 A (MACN-In 4097); Tierra del Fuego, 4 A (MACN-In 5777-1); Cueva del Indio, Puerto Deseado (MACN-In 36042); Sierra Grande, Río Negro province, in tide pools (MACN-In 36041); Punta Peñas, San Julián, Santa Cruz province, 2 m (MACN-In 36037); Playa La Mina, San Julián, Santa Cruz province intertidal (MACN-In 36038); Bahia Almanza, Puerto Harberton, Tierra del Fuego, 3 m (MACN-In 36043); San Antonio Oeste, Río Negro, intertidal, 3 A (MACN 35387); 54°47′36″ S, 64°22′35″ W, 1 A, R/V Eltanin Cruise 712, Sta. 71-2-44, 24 May 1971, intertidal (USNM 881127); 54°46′12″ S, 64°24′42″ W, 1 A, R/V Eltanin Cruise 712, Sta. 71-2-46, 21 May 1971, intertidal (USNM 881131); 54°4536″ S, 64°02′36″ W, 1 A, R/V Eltanin Cruise 7151, Sta. 869, 23 October 1971, intertidal (USNM 881132); 54°45′45″ S, 64°09′55″ W, 1 A, R/V Hero Cruise 712, Sta. 71-2-40, 21 May 1971, intertidal (USNM 881130); 54°47′48″ S, 65°16′ W, 1 A, R/V Hero Cruise 712, Sta. 71-2-8, 23 April 1971, intertidal (USNM 881126); 54°48′, 65°14′ W, 1 A, R/V Hero Cruise 712, Sta. 71-2-14, 25 April 1971, intertidal (USNM 881129); Punta Arenas, Cabeza de Mar, Chile (ANSP 101444); Ushuaia (ANSP 316762); Malvinas Is. (ANSP 277535 and 277538); Cape Fairweather, Santa Cruz province, Argentina (ANSP 78080); Straits of Magellan (ANSP 36241 and ANSP 366497); Puerto San Julián (ANSP 312324); Santa Cruz River (ANSP 101445); Puerto Gallegos (ANSP 312319); Golfo San Jorge (ANSP 178645); Puerto Madryn, Chubut (ANSP 170471); Puerto Parry, Isla de los Estados, 54°46′ S, 64°23′ W (ANSP 402810); mouth of Santa Cruz River (ANSP 88536); Punta Arenas (ANSP 88549); Puerto Madryn (ANSP 170474); Punta Arenas, Chile (ANSP 199711).

Distribution: *Trophon geversianus* has the widest geographic range of all species of *Trophon*, i.e., from Buenos Aires province to Burdwood Bank in the southwestern Atlantic, Tierra del Fuego and Malvinas Is., and the Magellan Strait in Chile. Literature records from around Antarctica are almost certainly wrong assignments, probably mistaking it for *Trophon nucelliformis* Oliver and Picken, 1984, *T. macquariensis* Powell, 1957, or *T. albolabratus* Smith, 1875.

Remarks: *Trophon geversianus* is the best-known species of the entire genus. The great morphological variation can be appreciated from the large number of names proposed for the different morphological variants

in this species. Zaixso (1973) and Penchaszadeh (1976) both studied the egg capsules of this species but only the latter confirmed the existence of short-lived nurse eggs in the capsules.

Trophon varians is a dubious species described by d'Orbigny from material he collected in northern Patagonia (*"au sud du Rio Negro"*). This species has no lamellae, weak spiral cords, and its shell is unusually thick. Houart (1998) illustrated a paralectotype (as syntype) housed in Paris and Aguirre (1993) designated and figured the lectotype (BMNH 1854.12.4.539) from 13 syntypes from the BMNH collection. According to d'Orbigny's illustration (Plate 42, figs. 4, 5) and the lectotype and the paralectotype housed in Paris, it appears that its distinctive characters are the thickness of the shell and absence of lamellae. However, despite this difference between *T. geversianus* and these primary types of *T. varians*, the rest of the paralectotypes are very similar to other thin-shelled specimens of *Trophon geversianus* usually found exposed during low tides in northern Patagonia, Golfo San Matías and around the Valdés Peninsula. The anatomy and radula of the latter are identical to those of *T. geversianus*. The specimens with heavy shells are characteristic of the mouth of Rio Negro. Nothing is known about the anatomy and radula of these heavy specimens. Perhaps these characters may prove that it is only a local variation of *Trophon geversianus*, as it was suggested originally by d'Orbigny himself (1841: 452). D'Orbigny (1841: 452; 1839, plate 42, figs. 6–7) also described and illustrated the egg-capsules from what he supposed were *T. varians*. The illustration agrees better with capsules of *Urosalpinx haneti* (Petit, 1856).

Trophon plicatus (Lightfoot, 1786)
(Figures 22–42)

Le Sabot Magellanique Favanne, 1780: 342, pl. 79, fig. I., *nomen nudum.*
Buccinum laciniatum Martyn, 1784: fig. 42, *nomen nudum.*
Murex plicatus Lightfoot, 1786: 104.
M. lamellosus Martyn.—Gmelin, 1791: 3536; Wood and Hanley, 1856: 133, pl. 27, fig. 100
Polyplex gracilis Perry, 1811: pl. 9, fig. 4.
Fusus laciniatus Martyn.—Reeve, 1847: spec. 14, figs. a, b, c.; Hupé *in* Gay, 1854: 168; Gould, 1861: pl. 16, fig. 278.
Trophon laciniatus Martini.—H. and A. Adams, 1853: 77, pl. 8, figs. 3 a, b.; Kobelt, 1878: 280, pl. 72, figs. 6, 7; Tryon, 1880: 143, pl. 31, figs. 330–332. Rochebrune and Mabille, 1889: H.53; Strebel, 1904: 199, pl. 3, figs. 1–8; Lamy, 1906: 3; Strebel, 1908: 37; Castellanos, 1970: 74, pl. 5, fig. 1.
?*Trophon antarcticus* Philippi, 1868: 225 (sensu Tryon 1880).
T. lacineatus Martyn. Sowerby II, 1880: pl. 404, fig. 13.
T. (Stramonitrophon) laciniatus (Martyn).—Powell, 1951: 156, fig. L, 86.
T. (Stramonitrophon) lamellosa (Gmelin).—Dell; 1971: 212.
T. plicatus (Lightfoot, 1786).—Rehder, 1967: 20; Cernohorsky, 1977: 117, fig. 18; Vokes, 1991: 7, fig.; 1991b: 9, figs. 14–16; 1992: 3, figs. 2, b, c, d.; Castellanos and Landoni, 1993: 5, figs. 16, 15, 22.

Description: Shell of medium to large size (to 50 mm), smooth, fusiform, thin, somewhat chalky; protoconch smooth of 2½ whorls; teleoconch of 6 shouldered whorls, spire less than ½ of total shell height. Spire angle about 50°; suture impressed; subsutural ramp straight, aperture small, ovoidal, interior pale brownish; anterior siphonal canal long (more than half height of the aperture), narrow, curved, open; umbilicus absent; outer lip rounded with reflected edges; inner lip curved, adpressed. Axial ornamentation of irregular, low lamellose varices in the first whorls, that become 8–10 real lamellae in the last ones. Lamellae growing over the entire whorl, but attached to the shell, sometimes curving adaxially. Lamellae ending in a peripheral spine, in some specimens growing adapically. Spiral ornamentation poorly developed to almost smooth, sometimes consisting of 6 weak cords on the base of the last whorl and the back of the siphonal channel. Regular, very weak growth lines present throughout shell.

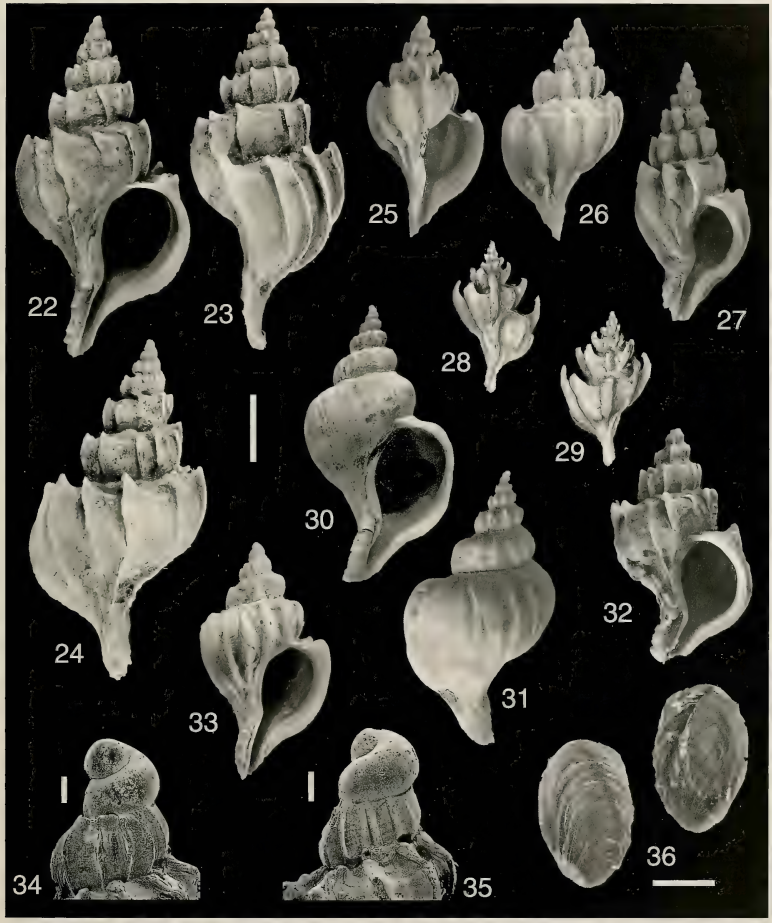
Shell ultrastructure composed of two layers; innermost layer (25% of shell thickness), composed of colabrally aligned crossed lamellar aragonite, outer layer thick (75% of shell thickness) with amorphous calcite (Figure 42).

Operculum oval, with terminal nucleus. External surface covered by concentric, irregular, growth lines. Inner surface attachment area with two or three horseshoe-shaped scars, glazed rim present in all specimens (Figure 36).

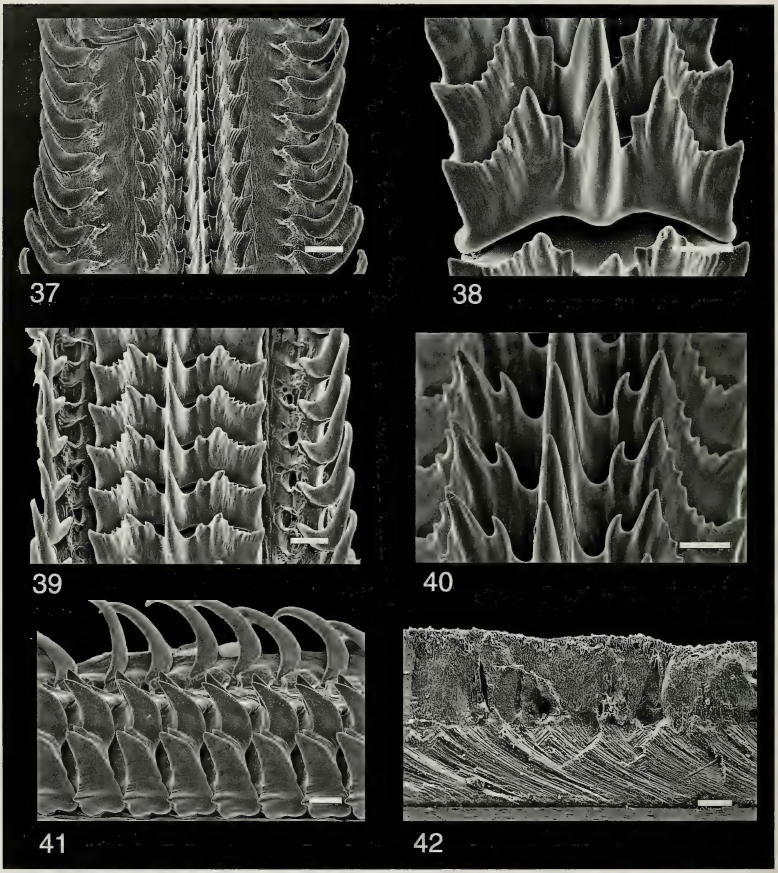
Animal of medium size relative to shell. Mantle large, mantle roof thin. Cephalic tentacles broad in basal half, flat, blunt, with rounded large black eyes in the middle; mantle edge thickened, smooth; pallial organs arranged as in other rachiglossans; brown osphradium less than half of ctenidium length, slightly asymmetrical, with 50–55 leaflets per side; ctenidium as wide as osphradium, containing triangular leaflets. Hypobranchial gland brownish and inconspicuous, rectum to the right of hypobranquial gland.

Proboscis pleuroembolic, long, broad. Radular ribbon extending beyond rear of buccal mass, long (0.69 × aperture height vs. 0.78 × aperture height in *Trophon geversianus*). Esophagus loops beneath buccal mass, where esphagus receives embedded ducts of salivary glands anterior to a small Leiblein valve. Esophagus curving distinctly and running along entire side of gland of Leiblein. Esophageal glands (*"Glandule framboise"*) whitish in color, posterior to nerve ring slightly marked on the external side of the esophagus. Large salivary glands enveloping Leiblein valve and accessory salivary glands. Accessory salivary glands distinctly large, sometimes dark-colored, tubular, compact, coiled, embedded in salivary glands. Gland of Leiblein conspicuous, brown, ending in a medium size blind duct and very small ampulla.

Radula rachiglossan with rachidian teeth wide (~150 µm), central cusp thin, large; lateral cusps wider and slightly shorter than central cusp, with inner edge straight; with sharp straight denticle in upper third of internal edge of lateral cusp, external edge with 6 very



Figures 22–36. *Trophon plicatus* (Lightfoot, 1786). **22–24.** MACN-In 36033, Bahía Ensenada, Ushuaia, Tierra del Fuego, Argentina. **25–26.** MACN-In 9032-16, Comodoro Rivadavia, Chubut province, Argentina. **27.** BMNH 19990384, 45°55.219′ S, 73°39.522′ W, intertidal, Islet NE shore of Isla Huemules, Golfo Elefantes, Chile. **28–29.** AK 133035, Station WS788 Discovery, 45°07′ S, 65°W. **30–31.** MACN-In 36034, Punta Peñas, San Julián, Santa Cruz province, Argentina. **32.** Same lot as Figure 6. **33.** MLP 27202, Bahía Golondrina, Ushuaia, Tierra del Fuego. **34–35.** Two protoconchs, scale bars = 400 μm. **34.** USNM 870535, 52°30′ S, 67°14′ W, in 82 m. **35.** USNM 901620, 53°35′ S, 69°45′ W, 1 D, R/V Hero Cruise 692. Sta. 404, 37–46 m. **36.** MLP 27232, operculum, external (left) and internal (right) views, scale bar = 1 cm. Scale bar for all shells = 1 cm.



Figures 37–42. *Trophon plicatus* (Lightfoot, 1786). **37.** MLP 27232, Dorsal view of radular ribbon. Scale bar = 50 μm. **38.** MLP 526, San Julián, Punta Peñas, 1 March 1924, rachidian teeth. Scale bar = 30 μm. **39.** Variations of rachidian teeth, Rocamora, Ushuaia, 1 A, 8–10 m (MACN-In 36053). Scale bar = 30 μm. **40.** MLP 27202, Bahia Golondrina, Ushuaia, Tierra del Fuego, Argentina, detail of the rachidian teeth. Scale bar = 20 μm. **41.** Same specimen as 40, lateral view of rachidian teeth, scale bar = 30 μm. **42.** USNM 870535, 52°30′ S, 67°14′ W, in 82 m, shell ultrastructure, fracture surface commarginal. Scale bar = 30 μm.

well defined denticles, always present. Base of rachidian tooth sinuous, sliding beneath base of next tooth. Marginal area with single conspicuous cusp. Lateral teeth with single, long and narrow cusp, slightly attached basal plate. Cusps of rachidian teeth pyramid-like in lateral view (Figures 38–40).

Male and female organs as in *Trophon geversianus* (see Harasewych, 1984).

Type Locality: Islas Malvinas.

Type Material: Probably lost. According to Dance (1966) part of the material from the Portland Catalogue is in London (BMNH), however this is not the case of *T. plicatus*.

Additional Material Examined: 52°30′ S, 67°14′ W, 2 D, R/V Eltanin Cruise 11, Sta. 980, 14 February 1964, 82 m (USNM 870535); 53°35′ S, 69°45′ W, 1 D, R/V Hero Cruise 692, Sta. 404, 37–46 m (USNM 901620); 52°56′ S, 75°00′ W, 1 D, R/V Eltanin Cruise 11, Sta. 958, 5 February 1964, 92–101 m (USNM 870423); 53°06′ S, 67°04′ W, 3 D, R/V Hero Cruise 702, Sta. 450, 5 March 1970, 86 m (USNM 901622); 53°39′24″ S, 70°55′30″ W, 1 D, R/V Hero Cruise 702, Sta. 467, 25 April 1970, 24 m (USNM 901623); 52°35′ S, 65°08′ W, 1 D, R/V Eltanin Cruise 11, Sta. 976, 13 February 1974, 128 m (USNM 870525); 46°04′ S, 83°55′ W, 1 A, R/V Eltanin Cruise 25, Sta. 326 9 October 1966, 298 m (USNM 901621); 53°48.7′ S, 70°24.1′ W, 1 D, R/V Hero Cruise 702, Sta. 489, 29 April 1970, 13–18 m (USNM 901624); 53°32′ S, 64°57′ W, 2 A, R/V Eltanin Cruise 11, Sta. 974, 12 February 1964, 119–124 m (USNM 881960); 53°39′ S, 70°55.5′ W, 1 A, R/V Hero Cruise 702, Sta. 466, 20 m (USNM 901754); Bahia Golondrina, Ushuaia, 1 A, (MLP 27202); Rocamora, Ushuaia, 1 A, 8–10 m (MACN-In 36053); Bahía Ensenada, Ushuaia, Tierra del Fuego, (MACN-In 36033); 45°07′ S, 65°W, 1 A, Discovery Station WS788, 13 December 1931, 82–88 m (AK 133035) illustrated in figs. 28–29; Comodoro Rivadavia, 17 D (MACN-In 9032-16); 54°34′ S, 64°00′18″ W, 1 D, 1 A, R/V Hero Cruise 715, Sta. 870, 24 October 1971, 84 m (USNM 881128); Bahía Buen Suceso, 1 A, 23 October 1941, (MLP27230); Cabo Colnett, Isla de los Estados, 1 A, R/V Hero Cruise 712, Sta. 853, 20 October 1971, 91 m (USNM 869720); 2 D, 78 m (USNM 96176); Orange Harbor (USNM 5676); Paso Richmond, Tierra del Fuego 55 m, (MACN-In 24940); 55°7′ S, 66°33′ W, 82 m (MACN-In 23938); Tierra del Fuego (MACN-In 5240-2); Punta Peñas, San Julián, Santa Cruz province, Argentina, 4 A (MLP 27232); Punta Peñas, San Julián, Santa Cruz, Argentina, 1 A (MLP 27212); Puerto San Julián, Santa Cruz province, Argentina (49°15′ S, 67°39′ W), 4 A, 2–3 m (MACN-In 36034); 45°55.219′ S, 73°39.522′ W intertidal, Islet NE shore of Isla Huemules, Golfo Elefantes, Chile (BMNH 19990384).

Distribution: This is a typical species from the Magellanic province. It has been recorded from Peninsula Valdés to Tierra del Fuego in Argentina and Chile to 49°S in the north (Reid and Osorio, 2000).

Remarks: The authorship of the name according to Dance (1962) and Rehder (1967) should be credited to J. Lightfoot, the anonymous compiler of the "Catalogue" where the name was used for the first time, not to Solander.

There is an interesting range of conchological variation in *Trophon plicatus*, from almost smooth specimens to highly lamellate. However, the profile is always slender. *Trophon bahamondei* McLean and Andrade, 1982, is a morphologically similar species, with peripheral spines and shallow lamellae. On the other hand, *T. bahamondei* has no spiral ornamentation and *Trophon plicatus* has 6 weak cords on the base of the last whorl and the back of the siphonal canal.

The gross anatomy is that customary for most Patagonian Trophoninae. However, a distinctive anatomical feature is the morphology of the accessory salivary glands, which are compact, tubular, somewhat coiled and large, and completely embedded in the salivary glands. Most Patagonian Trophoninae (e.g., *T. bahamondei* as well as *T. geversianus*), have small, kidney-shaped, accessory salivary glands.

Radular features of *T. plicatus* are clearly different from *T. bahamondei* (see Figures 26–27). The latter has a distinctive small cusp on the outer margin of the lateral cusp on the rachidian teeth. In addition, the rachidian base is thinner and wider.

Trophon antarcticus Philippi, 1868, is probably a synonym according to Tryon (1880); however, the type material is missing and the description is rather obscure.

Powell (1951) described the subgenus *Stramonitrophon* to include only *T. plicatus* [(as *T. laciniatus* Martyn, *nomen nudum* rejected by Opinion 456 (ICZN, 1957)] a species with *Stramonita*-like radula, i.e., rachidian teeth with three cusps, where the marginal side of the lateral cusps bears several denticles. This radula illustrated by Powell (1951: 194, fig. L, 86) was dissected from the specimen illustrated in figs. 28–29. The radular morphology of *T. plicatus* is different from that of *T. geversianus*. However, *Coronium coronatum* (Pennant, 1777) (Neme and Leme, 1978) and *T. acanthodes* Watson, 1882, bear the same denticles on the lateral cusps of the rachidian teeth. This appears to be a common feature in several Trophoninae from the southwestern Atlantic.

The shell of *Trophon iarae* Houart, 1998, shows some similarity with some specimens of *T. plicatus*. It was based on only two specimens collected by fishing boats apparently from Brazil and off Uruguay. The anatomy and soft parts of *T. iarae* remain unknown. The radula apparently has been illustrated by Calvo, 1987 (although according to Houart, 1998: 127, there is no certainty about the identity of the specimen from where this radula was taken). In any event, this illustration does not allow for a detailed comparison with other species. Further comments about the validity of this species or its

affinity with other species of *Trophon* mostly depends on anatomical data which are not available.

Houart (1998: 127) mentioned the specimen of *T. plicatus* illustrated by Cernohorsky (1977) from Lively Is. (Malvinas Is.) as belonging to his new species, *T. iarae*. However, Cernohorsky's specimen could be easily included in the range of geographic distribution and morphological variation of *T. plicatus*. He also illustrated two specimens of *T. patagonicus* as *T. plicatus* (Figures 8–10 in Houart, 1998).

Trophon patagonicus (d'Orbigny, 1839)
(Figures 43–65)

Murex patagonicus d'Orbigny, 1839: pl. 62, figs. 2–3; 1941: 452
non Fusus patagonicus Sowerby, 1846 (=*Trophon*).
Trophon necocheanus Thering, 1907: 404, pl. 16, fig. 106.
Trophon laciniatus (Martyn).—Carcelles, 1946: 70–72, figs. 6 a, b, 7 a–d, 8.
Trophon plicatus (Lightfoot, 1786).—Rios, 1985: 88, pl. 31, fig. 386; 1994: 114, pl. 37, fig. 483; Houart, 1998: 130, figs. 8–10 *non* Lightfoot, 1786.

Description: Shell large (up to 72 mm), biconic, heavy, chalky or glossy white, sometimes brownish grey, opaque; protoconch smooth of 2¼ (~2.0 × 1.5 mm) asymmetrical whorls; transition to teleoconch well defined; teleoconch of 7 shouldered whorls, spire less than ⅓ of total shell height. Spire angle about 70°; suture impressed; aperture oval, interior glossy white; anterior siphonal canal rather long for the genus (half height of aperture), narrow, open; pseudoumbilicus deep and widely open; outer lip reflexed. Axial ornamentation of irregular strong, sharp lamellae covering entire whorl surface, numbering 9–12 in the last whorl. Continuum of morphologies present from completely smooth shells with no axial ornamentation (Figures 53–56), to some incipient lamellae along peripheral keel (Figures 48–50), to strongly developed lamellae (Figures 43–45). Spiral ornamentation missing, except on first teleoconch whorl which bears 3–4 invariably present spiral cords (Figures 62–63). Irregular growth lines present throughout shell surface. Some uncommon specimens have about three weak greenish or dark spiral lines on the last three or four whorls.

Shell ultrastructure arranged invariably of two layers; innermost layer (25% shell thickness), composed of crossed lamellar aragonite, outer layer very thick (75% shell thickness) of amorphous calcite (Figure 61).

Operculum oval, with terminal nucleus. External surface covered by concentric, irregular, growth lines. Inner surface attachment area with two or three horseshoe-shape scars.

Rachiglossan radula with rachidian teeth distinct, central cusp thin, large; lateral cusps slightly shorter than central cusp, sharp straight denticle in the upper third of the internal edge of the lateral cusp, external edge of lateral cusps smooth. Base of rachidian tooth sinuous, sliding beneath base of next tooth. Marginal area with single conspicuous cusp. Lateral teeth with single, long and narrow cusp, attached to basal plate (Figures 64–65).

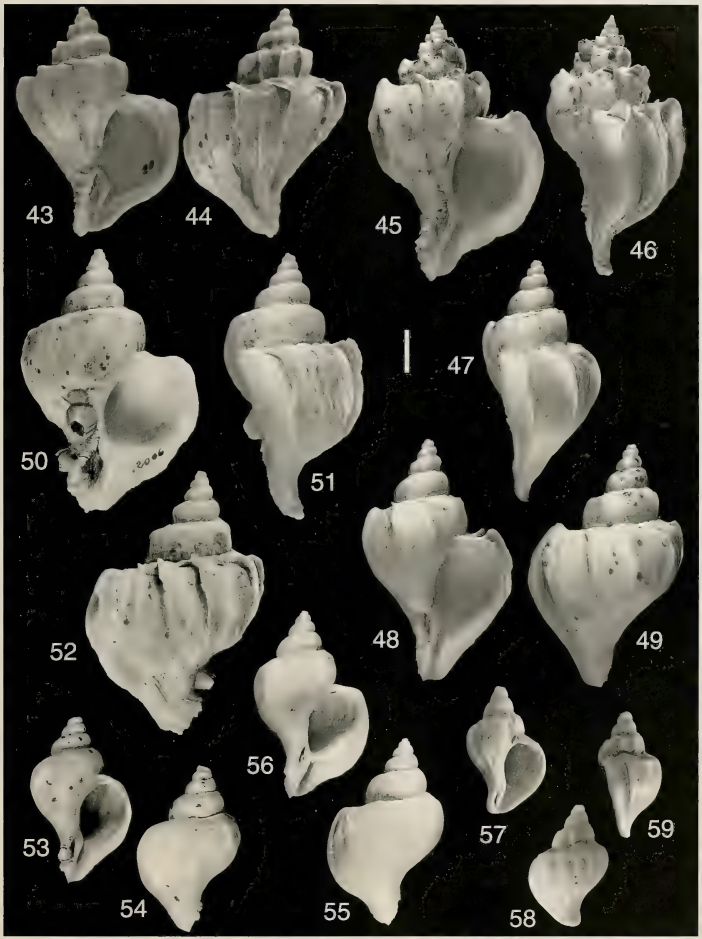
Penchaszadeh (1976) described the egg capsules of *T. patagonicus* [identified as *T. laciniatus* (Martyn) and *T. varians* (d'Orbigny)].

Type Material: Four syntypes are housed in the Natural History Museum, London under the number 1854.12.4.538, from "*Baie de San Blas, Patagonie*". One of them is herein illustrated (Figures 43, 44).

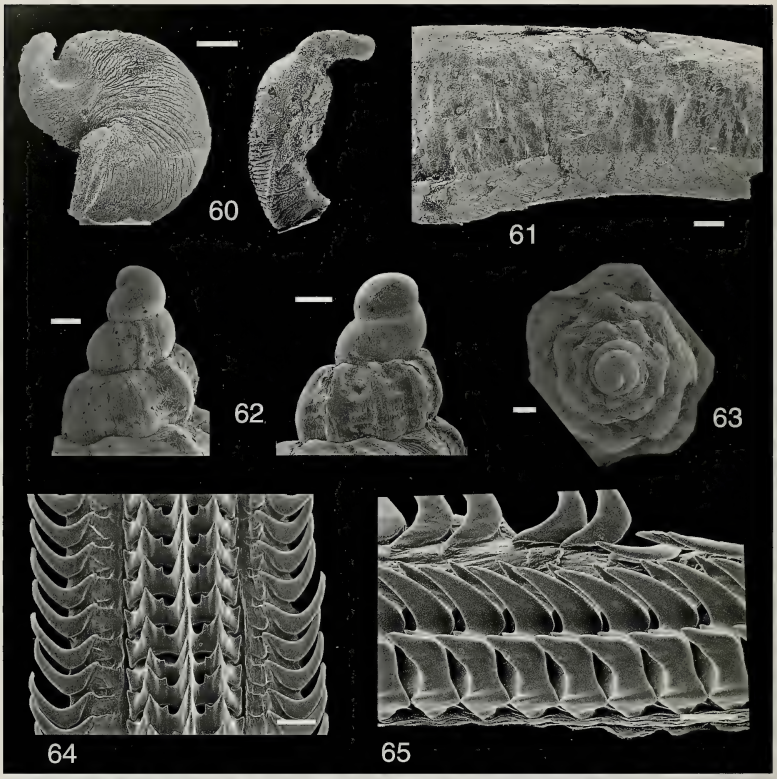
Additional Material Examined: Puerto Quequén, Buenos Aires province, 3 A (MLP 26309); Miramar, Buenos Aires province, 1 A, 1 D (MLP 417); Necochea, Buenos Aires province, 3 A, 30 m (AMNH 173640); Necochea, 1 A, 30 m (AMNH 181220); Puerto Quequén (ANSP 236034 and 236032); 18 miles off Puerto Quequén, 4 D (MACN-In 20441); 37°20′ S, 56°50′ W, 4 D, 55 m (MACN-In 15104); Mar del Plata, Buenos Aires province, Argentina (MACN-In 10289; 12902; 2 D, 45 m, 9361-51; 7 D, 11374; 11587; 11587-1; 4 D, 10249; 10320; 2 D, 10742; 11118; 3 D, 12066; 3 A, 25775; 9361-53; 5 D, 10290; 10190; 10248; 12216); 36°25′ S, 54°38′ W, 54 m, 1 D (MACN-In 23426); 34°40′ S, 52°18′ W, 1 A, 100 m (MACN-In 23491); Fondos de Querandí, Buenos Aires province, 5 A (MACN-In 14334); 25 miles off Puerto Quequén, 22 D (MACN-In 21138); Fondos de Querandí, 1 D (MACN-In 25774); Necochea, 2 D, 40–50 m (USNM 710024); Mar del Plata, 4 D, 1 D (USNM 568240; USNM 346826); off Necochea, 1 A, 30 m (USNM 876123, Bledsoe collection); Mar del Plata, 1 D (USNM 363768); Uruguay, 1 D (USNM 346786); 1 D, 36°30′ S, 54°44′ W, 26 m (MACN-In 24259).

Distribution: This species is common on the mussel banks off southern Uruguay and Buenos Aires province in depths of 25–40 m.

Remarks: *Trophon patagonicus* is a variable species, endemic to the littoral of Buenos Aires province and the Uruguayan coast. The species has had quite a confusing taxonomic history. Those specimens with well-developed lamellae have been usually identified as *T. plicatus*, and those with smooth shells and no ornamentation as *T. geversianus* or *T. varians*. Specimens collected on the same location were identified as two different species according to the presence or absence of lamellae. However, some specimens (Figures 50–52) are clearly intermediate forms, and no another anatomical feature seems to separate them. There is no reason to consider them as two different species. The whole lot of specimens studied by Carcelles (1946) shows clearly that he confused d'Orbigny's species with *T. plicatus*. Such a mistake was also made by Rios (1985, 1994) and several other authors. *Trophon plicatus* is a typical magellanic species with a thinner and more cylindrical profile, medium size (never reaching more than 50 mm high). Specimens of *T. plicatus* here identified were never collected at latitudes north of 45°S. Its protoconch is always smooth and with fewer whorls, and the lamellae along the keel usually develop into strong triangular projec-



Figures 43–59. *Trophon patagonicus* (d'Orbigny, 1839). **43–44.** Syntype BMNH 1854.12.4.538, Bahía San Blas, Argentina. **45–46.** MACN-In 36040, Puerto Quequén, Buenos Aires. **47–49.** MLP 417, Miramar, Buenos Aires, in 54 m. **50–52.** MACN-In 12066, Mar del Plata, Buenos Aires. **53–56.** MACN-In 36031, Puerto Quequén. **57–59.** MACN-In 21047, "Carmen de Patagones?", Buenos Aires. Scale bar for all figures = 1 cm.



Figures 60–65. *Trophon patagonicus* (d'Orbigny, 1839). **60.** Penis, critical-point dried. Lateral and frontal view. Scale bar = 1000 μm. **61.** Shell ultrastructure, fracture surface commarginal. Scale bar = 300 μm. **62–63.** MACN-In 11374, protoconch, three views, Mar del Plata, Buenos Aires province. Scale bar for all figures = 600 μm. **64.** Dorsal view of radular ribbon. Scale bar = 50 μm. **65.** Lateral view of rachidian teeth. Scale bar = 50 μm.

tions approximately parallel to the coiling axis. The aperture is larger and subcircular in *T. patagonicus*, very different from the smaller and almost circular one on *T. plicatus*. *Trophon geversianus* usually has strong spiral ornamentation on the entire shell surface, a feature also observed in *T. varians*.

Ihering (1907) described *T. necocheanus* based on (Quaternary?) specimens collected at Necochea, Buenos Aires province, Carmen de Patagones, Buenos Aires province, and Sierra Laziar, Santa Cruz province ("*Formation araucanienne*"). Most of the type material is lost, but the remaining types fall within the range of variation of *T. patagonicus*. One of the specimens, from a lot of three, with uncertain locality (MACN-In 21047, relabeled "Carmen de Patagones?") is here illustrated (Figures 57, 59). This specimen was acquired through an exchange with Museu Paulista, São Paulo, Brazil (where Ihering worked for most of his professional life) and is

part of the original type series. All of the specimens fit well in the original description of *T. patagonicus* and there is no doubt that is the same species described by d'Orbigny.

Sowerby II (2nd of name) described in 1846 *Fusus patagonicus* from the Tertiary of San Julián (Santa Cruz province, Argentina), a species that clearly belongs in *Trophon*. Therefore, as the two species are quite distinct, d'Orbigny's name has priority over Sowerby's (Griffin and Pastorino, 2005).

Trophon acanthodes Watson, 1882
(Figures 66–78)

Trophon acanthodes Watson, 1882: 386; 1886: 166, pl. 10, fig. 6; Cernohorsky, 1977: 112, fig. 9 (holotype); Pain, 1980: 8, fig.; Rios, 1985: 88, pl. 31, fig. 388; Castellanos, 1986: 22, fig.; Castellanos and Landoni, 1993: 8, pl. 2, fig. 28.
Fusus acanthodes (Watson).—Carcelles, 1947: 12, pl. 2, figs. 1, 2; pl. 3, figs. 3, 4 (not figs. 5, 6 which is *Coronium coronatum*).
Pagodula acanthodes (Watson).—Kaicher, 1980: fig. 2599.
"Fusinus" acanthodes (Watson).—Calvo, 1987: 153, fig. 127.
"Trophon" acanthodes Watson.—Rios, 1994: 37, pl. 37, fig. 486.

Description: Shell large, about 125 mm high, thick, slender in profile, chalky white; protoconch worn in all specimens; teleoconch of 7 shouldered whorls; spire less than ⅓ of total shell height. Spire angle about 45°; suture impressed, subsutural shelf oblique, somewhat convex, aperture small, subcircular, interior glossy white; anterior siphonal canal very long (longer than aperture height) deep, straight or curved, always open; outer lip rather reflected, rounded, inner lip adpressed. Axial ornamentation of 12–15 regularly spaced, axial lamellae, slightly raised, almost attached along the entire whorl, producing open, conspicuous, regularly spaced spines at periphery; spines becoming more closely packed on last whorl. Spiral ornamentation of 4–5 weak rounded threads on the lower part of the first whorls, becoming more than 20 in last one. Growth lines present throughout shell, producing wrinkly surface by intersection with spirals.

Operculum elliptical, nucleus terminal, older specimens tear-shaped. External surface covered by concentric, irregular, growth lines. Inner surface with a conspicuous marginal rim; attachment area covering almost the whole operculum but the rim; horseshoe-shaped scars present.

Rachidian teeth wide (~130 μm), central cusp large; lateral cusps wider and shorter than central cusp, inner edge with an almost obsolete denticle (particularly in adult specimens), external edge with 5–6 denticles decreasing in size towards the edge. Base of rachidian tooth curved, somewhat sinuous, sliding beneath base of next tooth. Marginal area with single cusp. Lateral teeth with single, long cusp, slightly attached basal plate.

Shell ultrastructure composed of two layers: innermost layer (55% of total thickness of shell) composed of crossed lamellar aragonite, outer layer (45%) of amorphous calcite.

Animal as in other *Trophon* species but with some size differences. Tentacles long and well defined, joined at base; eyes deeply marked. Salivary and accessory salivary glands as in *T. plicatus*. Osphradium a bit more than one third of ctenidium length, asymmetrical, with about 112 leaflets, ctenidium with about 250 leaflets twice as large as osphradium. Typical pleuroembolic proboscis, shorter than in *T. geversianus*, valve of Leiblein also smaller; gland of Leiblein large with a long blind duct. Radula long; digestive tract with the usual loop on the left side of the gland of Leiblein, before the duct to the gland.

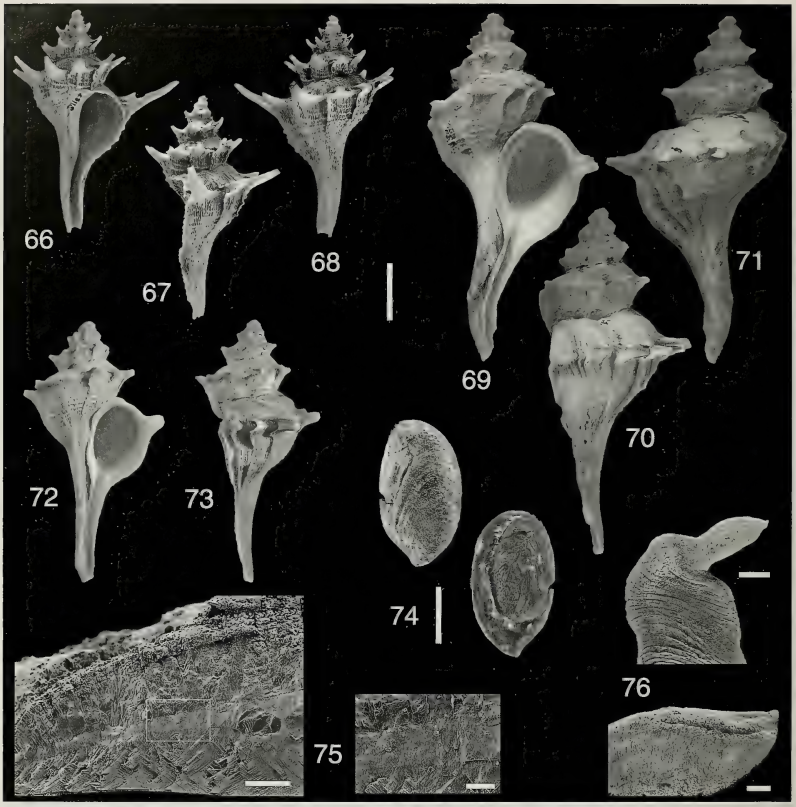
Male and female organs similar to *T. geversianus*.

Type Material: BMNH 1887.2.9.568, holotype 50°S′30″ S, 74°41′ W, 229 m (illustrated by Cernohorsky, 1977, fig. 9).

Additional Material Examined: 52°53′ S, 74°05′ W, 3 D, R/V Eltanin Cruise 23, Sta. 1605, 1 April 1966, 522–544 m (USNM 901756); off Mar del Plata, 5 A, January 1962 (MLP 26283); 52°41′ S, 74°35′ W, 1 D, R/V Eltanin Cruise 21, Sta. 290, 6 January 1966, 188–247 m (USNM 870115); 51°56′ S, 56°39′ W, 1 D, R/V Eltanin Cruise 7, Sta. 557, 14 March 1963, 855–866 m (USNM 870345); 52°52′ S, 75°18′ W, 1 D, R/V Eltanin Cruise 21, Sta. 288, 119–329 m (USNM 901758); 52°51′ S, 74°13′ W, 1 D, R/V Eltanin Cruise 21, Sta. 291, 523–539 m (USNM 901757); 52°53′ S, 74°05′ W, 2 D, R/V Eltanin Cruise 23, Sta. 1605, 1 April 1966, 522–544 m (USNM 897615); 40°15′ S, 57°40′ W, 1 A (MACN 18425); 40°03′ S, 57°00′ W, 1 D, 50 fathoms (91.5 m) (MACN 15699); 30 miles off Mar del Plata (ANSP 262989 and 236028); off Mar del Plata, 1 A, 2 D (MACN 17671 and 16449); 39°26′ S, 56°40′ W, 1 A, 1 D, 90 m (MACN 17040); 39°02′ S, 56°46′ W, 1 A, 1 D; East of Punta Médanos (39°–39°30′ S), 4 D, 50 fathoms (91.5 m) (MACN 14386); 39°55′ S, 57°50′ W, 1 D, 51 fathoms (93 m); 38°25′ S, 56°30′ W, 3 D (MACN 16798); 39°35′ S, 57°10′ W, 1 A, 1 D (MACN 18342); 39°50′ S, 57°18′ W, 4 A, 52 fathoms (95 m) (MACN 21741); 39°00′ S, 57°10′ W, 2 D, 45 fathoms (82 m) (MACN 15216); 37°15′ S, 54°50′ W, 1 A, R/V Aldebaran, March 2000, commercial otter trawl, 111 m (MACN-In 36032); 36°37′ S, 54°14′ W, 1 A, R/V Aldebaran, March 2000, otter trawl, 104 m (MACN-In 36031); 39°02′, 57°02′ W, 2 D, 46 fathoms (84.1 m) (MACN-In 25118); 37°35′ S, 54°55′ W, 1 D, 105 fathoms (192 m) (MACN-In 25165-2).

Distribution: Off Rio Grande do Sul state in Brazil (Rios, 1994), Uruguay, to Tierra del Fuego, Argentina.

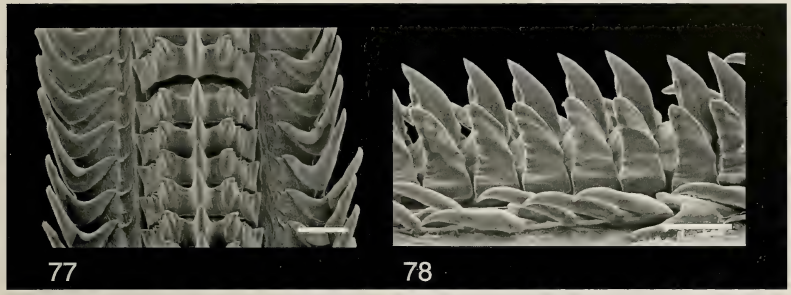
Remarks: The shell of *Trophon acanthodes* is somewhat similar to that of *Coronium coronatum*, which in fact could be granted that generic position. The operculum and the radula are different in both species. The operculum is somewhat triangular in *Coronium* with a weak rim instead of the characteristic thicker one of the *Trophon* species. The radula of *Trophon acanthodes* presents the intermediate cusp between the central and the lateral



Figures 66–76. *Trophon acanthodes* Watson, 1882. **66–68.** MACN-In 25118, 39°02′, 57°02′ W, 46 fathoms (84.1 m). **69–71.** MACN-In 36031, 37°15′ S, 54°50′ W in 111 m. **72–73.** MLP 26283, Mar del Plata. Scale bar for all shells = 1 cm.**74.** Two views of the operculum of the specimen in Figures 69–71. Scale bar = 1 cm. **75.** Ultrastructure of the shell. Scale bar = 200 μm; detail, large quadrangle. Scale bar = 50 μm. **76.** Penis, critical-point dried (scale bar = 600 μm) with detail of the efferent conduct (scale bar = 150 μm).

one of the rachidian teeth almost obsolete, while in *Coronium coronatum* it is very conspicuous. Castellanos (1986) drew a stereotyped radula of *T. acanthodes* where denticles are wrongly placed on the margin of the rachidian tooth instead of the inner edge of the lateral cusp.

The protoconch in *Coronium* is multispiral and extremely pointed, distinctive of the genus. All the studied specimens of *T. acanthodes* are worn; however, some of them show the sinuated line of a typical *Trophon* protoconch.



Figures 77–78. *Trophon acanthodes* Watson, 1882. **77.** MLP 26283, off Mar del Plata Radula of a large specimen, frontal view. Scale bar = 50 μm. **78.** Lateral view. Scale bar = 50 μm.

Trophon pelseneeri Smith, 1915
(Figures 79–93)

Trophon pelseneeri Smith, 1915: 92, pl. 2, figs. 6, 7; Rios, 1994: 115, pl. 38, fig. 484; Houart, 1991: 33.
Trophon sp.—Carcelles, 1944: 253.
Trophon orbignyi Carcelles, 1946: 81, pl. 12; Castellanos, 1970: 73, pl. 5, fig. 6.

Description: Shell small to medium in size (up to 35–40 mm), fusiform, slender, chalky, pinkish with 2 weak, diffuse reddish bands along the edge of last whorl lamellae; protoconch symmetrical, cylindrical, smooth, of 2½ whorls; teleoconch of 7 rectangular whorls, spire ⅓ of total shell height. Spire angle about 45°, suture impressed, subsutural shelf straight, aperture small, circular, interior glossy white; anterior siphonal canal long, open, straight, with the tip adaxially curved, equal to aperture height; umbilicus slightly open, sometimes only a narrow slit; outer lip reflexed to form lamellae; inner lip curved, with white adpressed callus. Axial ornamentation of 9–11 regular, low lamellae, covering entire whorl surface; lamellae forming a back-turned spine at periphery. Spiral ornamentation of 2 to 3 very weak threads in first whorls becoming more than 7 in last one, sometimes only visible along edge of last whorl lamellae. Siphonal fasciolae slightly oblique, always present.

Operculum triangular (tear-shaped), with terminal nucleus. External surface covered by irregular growth lines. Inner surface attachment area with horseshoe-shaped scars; glazed rim weak but present (Figure 88).

Radula rachiglossate with rachidian teeth wider than high, central cusp thin, in a different plane than laterals; lateral cusps wider and shorter than central cusp, with inner edge oblique; sharp straight denticle in the upper third of the internal edge of the lateral cusp, external edge with almost obsolete denticles numbering 3–4. Base of rachidian tooth slightly sinuous, sliding beneath base of next tooth. Marginal area with single conspicuous cusp. Lateral teeth with single, long and narrow cusp, slightly attached basal plate (Figures 92–93).

Type Material: [*T. pelseneeri*] BMNH 1915.4.18.276–7, two syntypes from west of Malvinas Is. in 229 m (Figures 79–82) and [*T. orbignyi*] MACN-In 24421, Puerto Quequén, Buenos Aires, holotype (Figures 83–85) and 10 paratypes.

Additional Material Examined: Macaé, Rio de Janeiro, Brazil, August 1969, 2 A, 55 m (USNM 846550); Macaé, Rio de Janeiro, Brazil, 1 A, 30 m (AMNH 187586); Rio de Janeiro, Brazil, 1 A (AMNH 241045); off Rio de Janeiro, Brazil (ANSP 289807); 34°48′7″ S, 54°21′9″ W, 1 A, R/V Aldebaran, Cruise 9901, Sta. 25, 27 January 1999, 25 m, with Piccard trawl (MNHNM 15400).

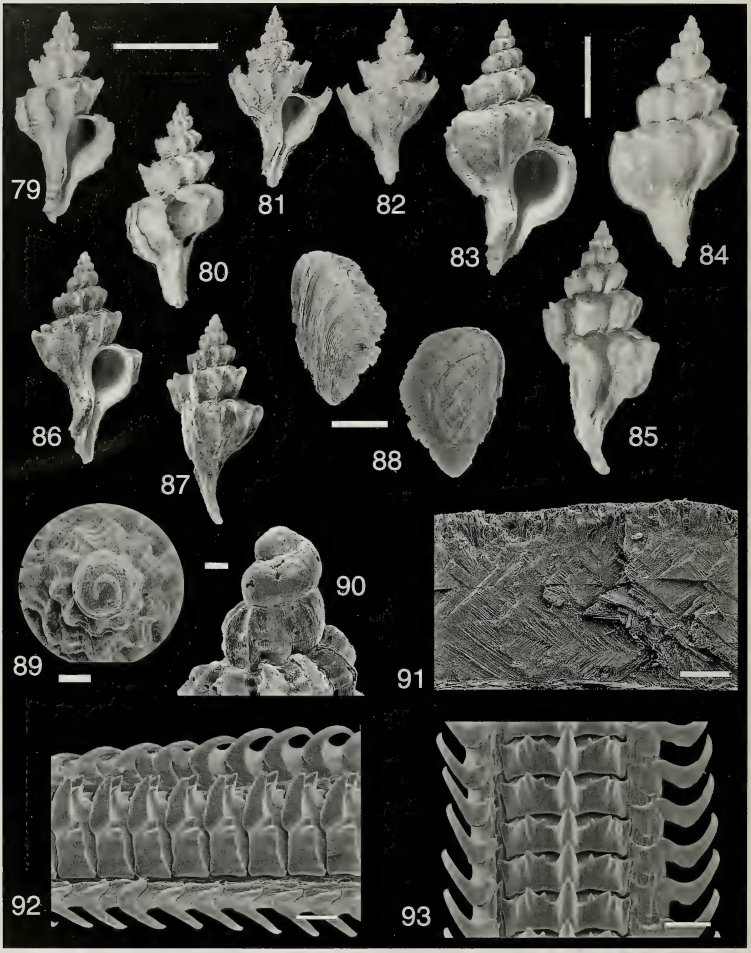
Distribution: Rio de Janeiro, Brazil, to Uruguay and Buenos Aires province, Malvinas Is. Rios (1994) cited it from dredgings from 55 to 225 m off the Brazilian coast.

Remarks: This is a rare species occasionally collected by fishermen on the mussel banks off Buenos Aires province. It was originally described from Sta. 38 of the British Antarctic ("Terra Nova") Expedition, west of Malvinas (Falkland) Islands in 125 fathoms depth. However, together with this species, the author mentioned several others not reported before or since from this latitude, but which occur at Station 42 of the same expedition, off Rio de Janeiro. This leads to the supposition that the material from these stations could have been mixed up (Scarabino, 2003: 199).

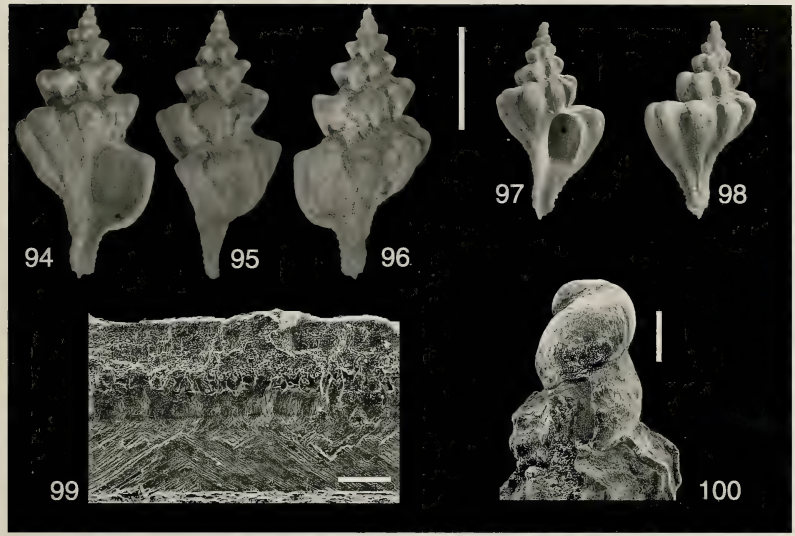
Trophon amettei Carcelles, 1946
(Figures 94–100)

Trophon amettei Carcelles, 1946: 84, fig. 13; Carcelles and Williamson, 1951: 287.

Description: Shell small in size (up to 30 mm), fusi-



Figures 79–93. *Trophon pelseneeri* E. A. Smith, 1915. **79–80.** BMNH 1915.4.18.276-7 syntype. **81–82.** BMNH 1915.4.18.276-7, other syntype. **83–85.** *T. orbignyi* Carcelles, MACN-In 24421 holotype. **86–87.** MNHNM 15400, B/I Aldebarán, 34°d48′7″ S, 54°21′9″ W, in 25 m. Scale bar = 1 cm. **88.** Two views of the operculum of the specimen in Figures 86–87. Scale bar = 2 mm. **89–90.** USNM 846550, apical and lateral view of the protoconch. Scale bars = 400 and 300 μm respectively. **91.** Detail of the ultrastructure of the shell. Scale bar = 100 μm. **92–93.** Dorsal and lateral view of the radula of the specimen in Figures 86–87. Scale bars = 30 μm.



Figures 94–100. *Trophon amettei* Carcelles, 1946. **94–96.** MACN-In 23810, holotype, 45°09′ S, 66°27′ W in 11.28 m. **97–98.** MACN-In 23810, paratype. Scale bar = 1 cm. **99.** MACN-In 23810, ultrastructure of the shell. Scale bar = 30 μm. **100.** MACN-In 23810, protoconch, uncoated SEM picture. Scale bar = 300 μm.

form, biconic, chalky whitish; protoconch elongate, smooth, of 2¼ whorls; teleoconch of 6 strongly shouldered whorls, spire less than ½ of the total shell height. Spire angle about 45°, suture impressed; subsutural shelf short but straight, aperture small, ovoid, interior glossy white; anterior siphonal canal comparatively long, almost same height as aperture, open and straight; umbilicus closed, inner lip adpressed. Axial ornamentation of 8 regular concave lamellae per whorl. Lamellae growing attached to entire whorl surface and producing concave spine along periphery. Spiral ornamentation of 2 cords in first teleoconch whorls that soon become obsolete on subsequent whorls. Last whorl with 6–10 cords on lower part. Shell ultrastructure composed of two layers, similar to *T. geversianus*. Operculum and soft parts unknown.

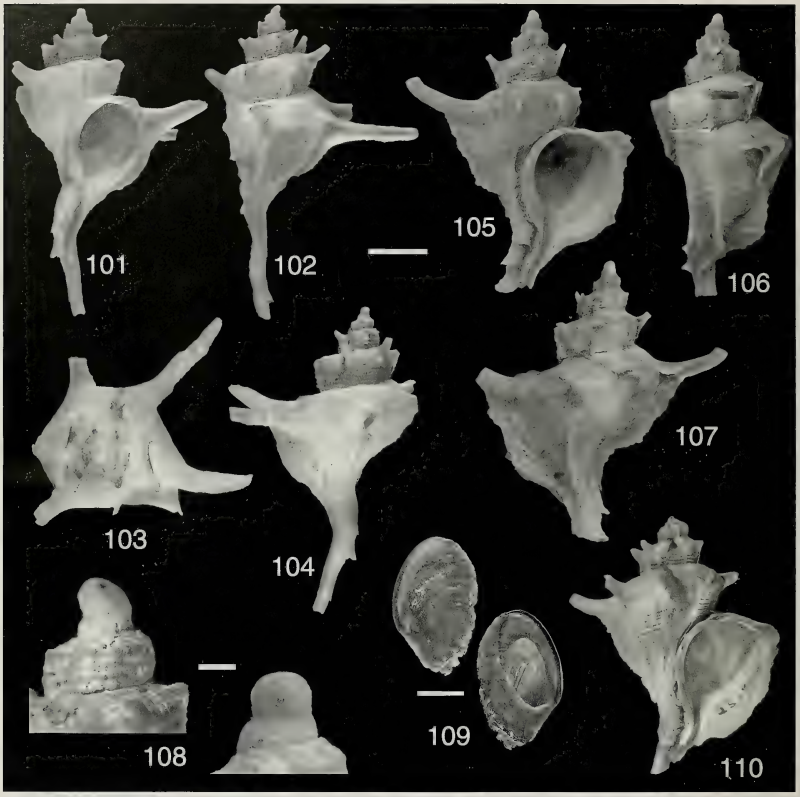
Type Material: Holotype and 15 paratypes (MACN-In 23810) all from 45°09′ S, 66°27′ W anchorage Restinga Aristizábal, Chubut province, in 8 fathoms (11.28 m), rocky bottom associated with the calyptraeids *Crepidula cachimilla* and *Calyptraea pileolus*.

Remarks: This is a rare species known only from the type locality. It has not been found again. The regular concave lamellae, are in fact, unusual for the genus. The protoconch resembles those usually found in the genus *Fuegotrophon*, however the typical fimbriate spiral ornamentation is absent. *Trophon pelseneeri* has a comparable profile, however it is easily segregated: where the latter has lamellae forming a back-turned spine at periphery, *T. amettei* presents a characteristic and unique concave lamellae. In addition *T. pelseneeri* has a slightly open umbilicus while in *T. amettei* it is invariably closed. Examination of the radula may beget a new generic allocation for this species.

Trophon clenchi (Carcelles, 1953)
(Figures 101–114)

Murex clenchi Carcelles, 1953: 7, figs. 23–28; Castellanos, 1970: 80, pl. 5, fig. 7; Fair, 1976: 31, fig. 15; Vokes, 1992b: 24; Rios, 1994: 115.
Poirieria (Poirieria) clenchi (Carcelles).—Vokes, 1970: 18.

Description: Shell medium in size, delicate, thin, chalky, translucent white; protoconch known only from the holotype, asymmetrical, globose, of 2–2½ whorls; teleoconch of 5 shouldered whorls; spire short, less than ¼ of total shell height. Spire angle about 45° (without spines); suture impressed, subsutural shelf short,

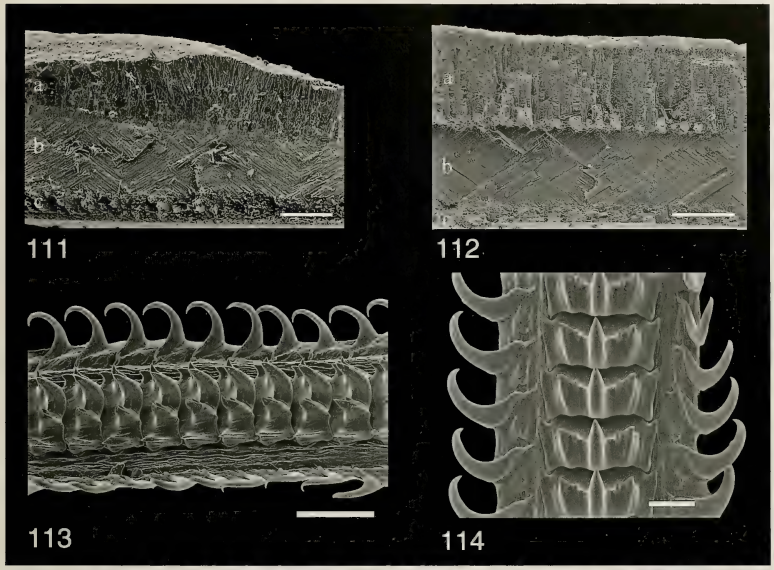


Figures 101–110. *Trophon clenchi* (Carcelles, 1953). **101–104.** MACN-In 25146, holotype, 38°24′ S, 55°36′ W in 89.61 m. **105–107.** MACN-In 36269, aproximately 45°10′ S, 57°20′. Scale bar = 1 cm. **108.** Holotype, protoconch. Scale bar = 1000 μm. **109.** External and internal views of operculum of specimen in Figures 105–107. Scale bar = 0.5 cm **110.** MACN-In 25146, paratype.

straight; aperture suboval, interior glossy white; anterior siphonal canal very long (longer than the aperture height), deep and slightly curved in the beginning and then straight, open but narrow; outer lip sharp, inner lip somewhat protruding, adpressed. Axial ornamentation of 7–9 regular axial lamellae growing across entire whorl surface, but attached to shell producing open, long and regularly spaced spines along periphery. Spiral ornamentation of 4–5 rounded cords on lower half of first whorls, becoming more than 20 in the last. Delicate growth lines present on entire shell surface.

Shell ultrastructure composed of two layers following the common pattern of the genus: innermost layer (40% of total thickness of shell) composed of crossed lamellar aragonite, outer layer (50%) of amorphous calcite. Sometimes, depending on the fracture mode, a basal aragonitic layer can be observed.

Radulae rachiglossate, rachidian teeth with three me-



Figures 111–114. *Trophon clenchi* (Carcelles, 1953). **111.** USNM 901774, 51°58′ S, 56°38′ W, R/V Eltanin Cruise 7, Sta. 558, 646–845 m, ultrastructure of the shell. Scale bar = 100 μm. **112.** *Poirieria zelandica*, ultrastructure, commarginal fracture surface. Scale bar = 100 μm. **113.** *Trophon clenchi* MACN-In 36269. Lateral view of radula ribbon. Scale bar = 100 μm. **114.** Dorsal view of radular ribbon. Scale bar = 50 μm.

dian cusps, the central one the larger and the lateral ones with a denticle, attached to the upper third of the interior margin of the lateral cusp; external margin with 2–3 obsolete denticles. Rachidian base sinuous, with the base offset under the proximal tooth. Marginal cusps single, never bifid. Lateral teeth curved, thin, with attachment area also thin (Figures 113–114).

Operculum triangular or suboval tear-shaped, attachment area elliptical, with horseshoe shape scars.

Type Material: 38°24′ S, 55°36′ W, off Mar del Plata, in 89.6 m, holotype and paratype (MACN-In 25146).

Additional Material Examined: 51°58′ S, 56°38′ W, 3 D, R/V Eltanin Cruise 7, Sta. 558, 646–845 m (USNM 901774), 41°51′ S, 57°34′ W, collected by Uruguayan fishermen, June 2002, 1062 m, 1A, MACN-In 36270; approximately 45°10′ S, 57°20′ Uruguayan fishermen, 1 A, MACN-In 36269; 54°50′ S, 63°50.5′ W, 2.5 miles south Punta Fallows, Isla de los Estados, Tierra del Fuego, 1 A, R/V Hero Cruise 715, Sta. 715/879, 28 October 1971, in 342–353 m (LACM 71-331).

Distribution: Known from off Buenos Aires province, Patagonia and Isla de los Estados, in 90–1050 m depth.

Remarks: Carcelles (1953) described *Murex clenchi* from two shells he received from the crew of the Ara Bahía Blanca, an Argentine Navy ship that occasionally collected material for the collection of the Museo Argentino de Ciencias Naturales (MACN). Both holotype and paratype were collected from the continental shelf off Buenos Aires province. This material remained housed at the MACN until it was sent on loan and it appears to have been lost for almost 30 years (see Castellanos, 1986). The return of the material to MACN made the type material again available for studies. Perhaps because of these facts, the ordinary quality of the illustration and the absence of soft parts, the species was always reluctantly considered as the southernmost representative of the genus *Murex*.

E. H. Vokes, in a fundamental paper published in 1970, stated that *Murex clenchi* belongs in the genus *Poirieria* sensu stricto. Rios (1994) considered *M. clenchi*

as an anomalous specimen of *Trophon acanthodes* Watson, a species that slightly resembles some specimens of *M. clenchi* (e.g., the paratype).

The morphology of the shell as well as the radula and penis of *Murex clenchi* allow the allocation in the genus *Trophon*. In fact, this was already suggested by E. H. Vokes (1992b). After studying the material of *T. acanthodes* housed at the MACN she proposed that *M. clenchi* belongs to *Trophon* sensu lato and not to *Poirieria*. It bears no relationship with *Poirieria* despite some apparent shell similarity. As it is shown in Figure 112, *Poirieria zelandica*, type species of *Poirieria*, has no calcitic layer on the shell but a thick aragonitic one instead (Figure 112a). In contrast, the entire group of Patagonian *Trophon* (*T. clenchi* in particular), shows different degrees of development of the typical calcitic layer on the distinct species.

The range of the very few lots studied falls within the geographic distribution of other species of *Trophon*. *Trophon clenchi* was known from two quite different geographic and bathymetric areas: off Buenos Aires province (in about 90 m) and the slope off Patagonia. A new lot is recorded here from Isla de los Estados, which significantly increases the range of distribution of the species. It is possible that like other Patagonian species of the genus, *T. clenchi* would be associated to hard bottoms, thus hampering the collection of material. Its fragility, size, and inadequate sampling of the area adds other reasons for the scarcity of records. It is suggested that these variables accounts for the disjunt recorded distribution of this species. In fact, this species started to be repeatedly collected recently, when the fishery of the Patagonian toothfish (*Dissostichus eleginoides*) on the Argentinean slope provided the opportunity to catch accidentally entangled specimens (F. Scarabino, pers. comm.).

Trophon wilhelmensis Ramirez-Bohme, 1981
(Figures 115–119)

Trophon (*Enixotrophon*) *wilhelmensis* Ramirez-Bohme, 1981: 6, fig. 1a, b.

Description: Shell of medium size, about 52 mm high, slender in profile, chalky white; protoconch unknown; teleoconch of 6 shouldered whorls; spire less than ⅓ of total shell height. Spire angle less than 45°; suture impressed, subsutural shelf straight, aperture small, subcircular, interior glossy white; anterior siphonal canal very long (longer than aperture height) deep, straight or curved, always open; outer lip rather reflexed, rounded, inner lip adpressed. Axial ornamentation of 12–15 regularly spaced, axial lamellae, slightly raised, almost attached along the entire whorl, producing open, conspicuous, regularly spaced spines at periphery; spines becoming more closely packed on last whorl. Spiral ornamentation of 4–5 weak rounded threads on the lower part of the first whorls, becoming more than 20 in last one. Growth lines present throughout shell, producing wrinkly surface by intersection with spirals.

Operculum elliptical, nucleus terminal. External surface covered by growth lines. Inner surface with marginal rim; attachment area, horseshoe-shaped scars present.

Rachidian teeth of about 90 μm wide, central cusp large; lateral cusps shorter than central cusp, inner edge with conspicuous denticle, external edge with 5 denticles of equal size. Base of rachidian tooth straight, somewhat sinuous, sliding beneath base of next tooth. Marginal area with single cusp. Lateral teeth thin with single, long cusp, slightly attached basal plate.

Type Material: Holotype in MNHN (unnumbered), 41°51′ S, 74°30′5″ W West of Chiloé Island in 250 m.

Additional Material Examined: Boca del Guafo, 43°39′36″ S, 73°51′11″ W, southern Chile, 6 July 2002, 1 A, 200 m (MNHN unnumbered).

Distribution: Known only from the holotype and another lot, both from the same area and depth, around the Chiloe Is., Chile.

Remarks: *Trophon wilhelmensis* was recently described from Chile with no mention of the similarity with *T. acanthodes*. Both species are actually quite similar. The species, known only from the holotype and another specimen, may be distinguished from *T. acanthodes* mainly by the upturned spines (compare Figures 66–73 with Figures 115–117). In addition, slight differences in the morphology of the rachidian teeth allow for further differentiation of the two species. Notwithstanding, future studies of specimens from intermediate localities could demonstrate that these represent but a single species.

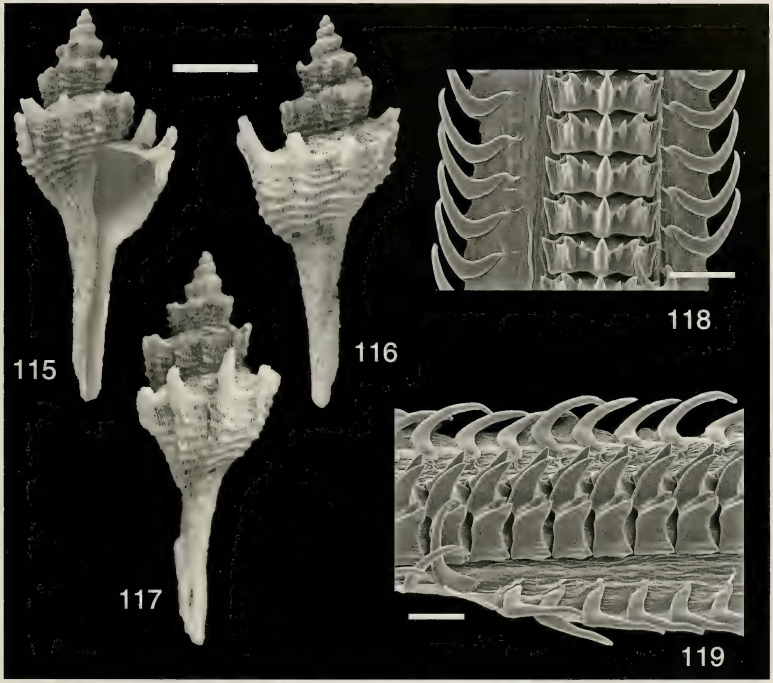
Trophon bahamondei McLean and Andrade, 1982
(Figures 120–125)

Trophon bahamondei McLean and Andrade, 1982: 10, figs. 24–25.

Description: Shell of medium size, up to 50 mm, slender, with narrow profile, chalky or creamy white; protoconch unknown (worn in all specimens); teleoconch of 6 shouldered whorls; spire less than ½ of total shell height. Spire angle about 45°; suture impressed, subsutural shelf well defined, straight; aperture subcircular, interior chalky white; anterior siphonal canal very long (equal to aperture height), narrow, and curved, open; outer lip sharp, rounded, inner lip adpressed. Axial ornamentation of 11–13 regular axial lamellae growing on entire whorl surface, but attached to the shell and producing open, short and regularly spaced spines along periphery. Spiral ornamentation lacking. Growth lines present throughout shell.

Operculum elliptical, nucleus terminal. External surface covered by concentric, irregular growth lines. Inner surface attachment area reaching upper side or center, with horseshoe-shaped scars (Figure 123).

Radula with rachidian teeth very wide (~114 μm), with narrow base, central cusp thin, large; lateral cusps



Figures 115–119. *Trophon wilhelmensis* Ramirez-Bohme, 1981. **115–117.** MNHNS unnumbered, Boca del Guafo, 43°39′36″ S, 73°51′11″ W, southern Chile, 6 July 2002, 200 m. Scale bar = 1 cm. **118–119.** Radula of the specimen on Figures 115–117, **118.** Frontal view. Scale bar = 50 μm. **119.** Lateral view. Scale bar = 40 μm.

wider and shorter than central cusp, inner edge with sharp, curved denticle, external edge with denticles decreasing in size toward lateral edge where they disappear. Base of rachidian tooth sinuous, inserted in part under base of subsequent tooth. Marginal area with single conspicuous cusp. Lateral teeth with single, long and very narrow cusp, slightly attached basal plate. Central cusps of rachidian teeth curved back in lateral view (Figures 124–125).

Animal very similar to *T. plicatus*. Osphradium less than half ctenidium length, asymmetrical, with 60–70 leaflets. Ctenidium with 140 leaflets less than two times larger than those of osphradium. Tentacles well defined; eyes deeply marked. Same type of accessory salivary glands, twisted and non-compact.

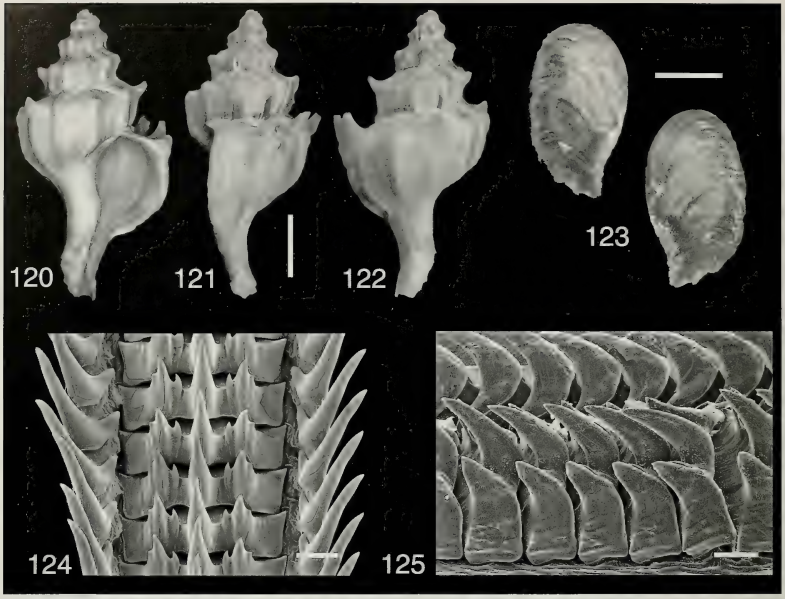
Male unknown, all specimens studied were females. Female similar to *T. geversianus*.

Type Material: Holotype from off Pichilemu, Chile, 34°27′ S, 340 m (LACM 1982, but apparently on loan) and two paratypes, 34°27′ S, 71°54′ W, 25 May 1976, 200–450 m (USNM 784739).

Additional Material Examined: 31°56′ S, 71°54′ W, off Los Vilos, Chile, 2 A, 8 March 1977, 240–350 m (LACM 72491); off Playa Blanca, Coquimbo, Chile, 400 m (ANSP 291065); off Coquimbo, Chile (LACM 75-88).

Distribution: This is a deep water *Trophon* known from latitudes 30° to 34° S off the coast of Chile.

Remarks: *Trophon bahamondei* is apparently a very



Figures 120–125. *Trophon bahamondei* McLean and Andrade, 1982. **120–122.** Paratype USNM 784739, 34°27′ S, 71°54′ W, Pichilemu, Chile, in 200–450 m. Scale bar = 1 cm. **123.** Operculum, external (right) and internal (left) views. Scale bar = 1 cm. **124.** Dorsal view of radular ribbon. Scale bar = 30 μm. **125.** Lateral view of rachidian teeth. Scale bar = 30 μm.

consistent species from the morphological standpoint. It was only recently described despite its apparently widespread presence in shrimp trawls. The deeper water habitat of species (more than 200 m) probably rendered the species less accessible in the past.

General morphology of shell and gross anatomy shows at first glance some similarities with those of *T. plicatus*; however close examination of shell and radula confirms the presence of a different species.

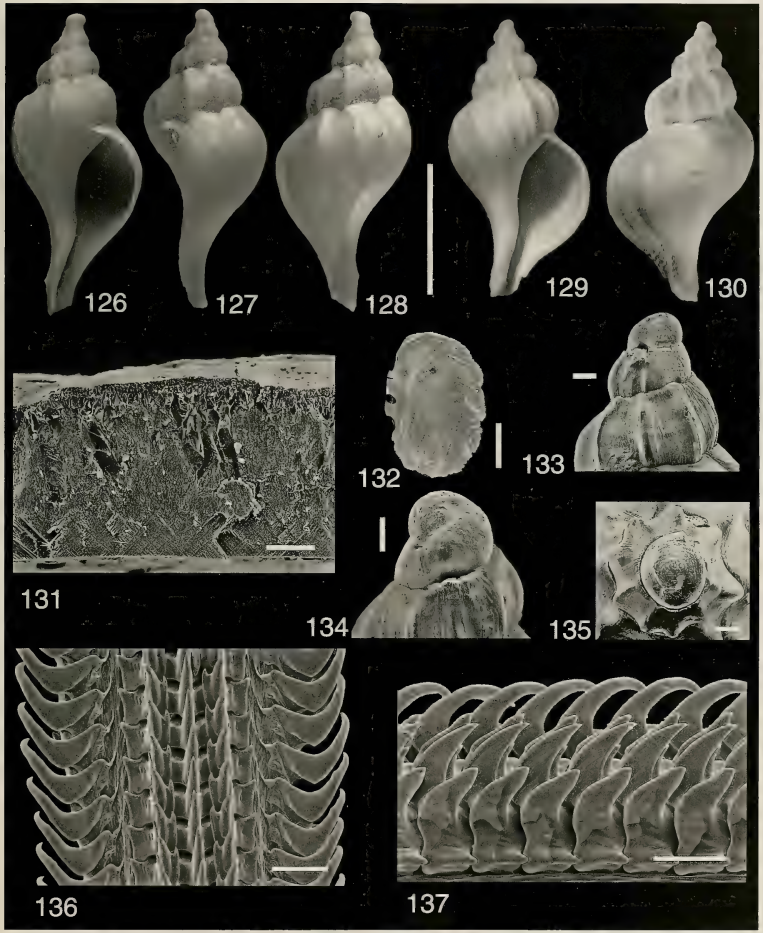
Trophon parodizi new species
(Figures 126–137, Table 1)

Description: Shell medium in size (up to 23 mm), very thin, chalky; protoconch smooth, of 1½ (1.41 × 1.39) very asymmetrical whorls; transition to teleoconch well defined; teleoconch of 4 convex whorls, spire less than ⅓ total shell height. Spire angle about 40°; suture impressed; aperture subovoid, interior glossy white; anterior siphonal canal medium in size (less than half height of aperture), narrow, open; umbilicus absent; outer lip rounded. Axial ornamentation of irregular, low, rounded ridges occupying entire whorl surface, numbering up to 9 in early whorls, but vanishing and undulate on last whorl. Spiral ornamentation poorly developed or almost smooth, when present consisting of obsolete, weak cords mostly developed on last whorl. Irregular growth lines present throughout shell.

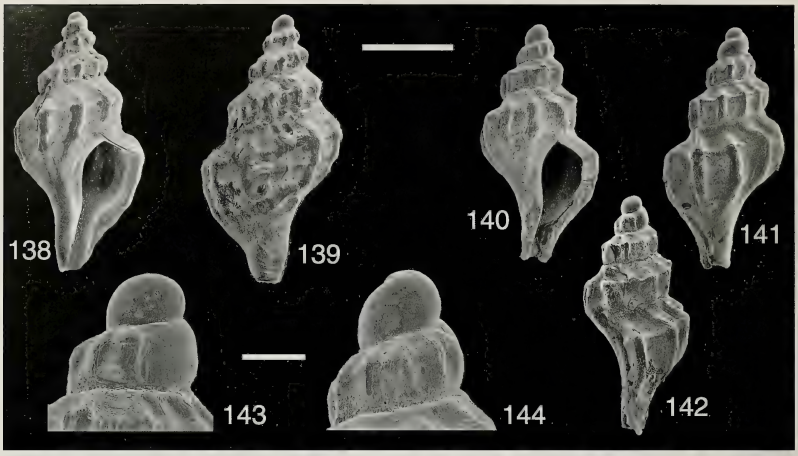
Shell ultrastructure composed of two layers; innermost layer thin (35% of shell thickness), composed of colabrally aligned crossed lamellar aragonite, outer layer thick (65% of shell thickness) with amorphous calcite.

Operculum oval, with terminal nucleus. External surface covered by concentric, irregular, growth lines. Inner surface attachment area with two or three horseshoe-shape scars. Animal unknown.

Radula rachiglossan with rachidian teeth distinctive, central cusp thin, large; lateral cusps almost same size as central cusp, sharp denticle on upper third, irregular external denticles present. Base of rachidian tooth sin-



Figures 126–137. *Trophon parodizi* new species. **126–128.** USNM 896397, holotype, 54°56′ S, 65°03′ W, in 229–265 m. **129–130.** USNM 896397, paratype, coated with ammonium chloride. Scale bar = 1 cm. **131.** Ultrastructure, fracture surface commarginal. Scale bar = 20 μm. **132.** USNM 896397, operculum, external view. Scale bar = 0.5 cm. **133–135.** Protoconch of the paratype, three views. Scale bar for all figures = 400 μm. **136.** Dorsal view of radular ribbon. Scale bar = 40 μm. **137.** Lateral view of rachidian teeth. Scale bar = 40 μm.



Figures 138–144. *"Trophon" malvinarum* Strebel 1908. **138–139.** NHRM 1041, holotype, 52°29′ S, 60°36′ W. **140–142.** MACN-In 23944-2, 55°07′ S, 66°33′ W. **143–144.** Protoconch. Scale bar = 400 μm.

uous, sliding beneath base of next tooth. Marginal area with a conspicuous cusp. Lateral teeth with single, long cusps and narrow, slightly attached basal plate.

Type Material: Holotype and one paratype from 54°56° S, 65°03° W, Le Maire Strait, R/V ELTANIN Cruise 11, Sta. 969, 10 February 1964, 229–265 m, Blake trawl (USNM 896397) (Map 1).

Material Examined: Only holotype and paratype.

Distribution: Known only from the type locality.

Etymology: This species is named after Juan José Parodiz, one of the pioneers of malacology in Argentina, Curator Emeritus at the Carnegie Museum, Pittsburgh, and a good friend.

Remarks: *Trophon parodizi* is an unusual species within *Trophon*. The small, very thin shell, almost completely smooth and devoid of lamellae, is an exception for the Patagonian *Trophon*. However, the radula and protoconch match those typical of the genus. The radular morphology resembles that of *T. plicatus* where the denticles of the lateral cusp of the rachidian teeth are placed along the entire external edge of the lateral cusp. In *T. parodizi* the lateral cusp is thinner and the denticles are more clearly separated from it and placed mainly along the marginal area as in *T. bahamondei*. In addition—a character also present in *T. bahamondei*—most internal denticle lies against the lateral cusp and is clearly differentiated from the rest.

"Trophon" malvinarum Strebel, 1908
(Figures 138–144)

Trophon malvinarum Strebel, 1908: 44, figs. 16 a–c; Carcelles and Williamson, 1951: 289; Castellanos and Landoni, 1993: 10, pl. 2, fig. 29.

Description: Shell small, up to 30 mm, thick, fusiform, profile slender, chalky, whitish; protoconch globose, somewhat cylindrical, with two whorls; teleoconch of 4½ shouldered whorls, spire less than ⅓ of total shell height. Spire angle about 45°; suture impressed; subsutural shelf abaxially oblique, aperture subquadrate, anterior siphonal canal moderately long (same height as aperture); umbilicus closed, outer lip polygonal to rounded; inner lip slightly curved, adpressed. Axial ornamentation of 8–9 regular, distinct low varices, which never develop into full-fledged lamellae. Spiral ornamentation of about 3 cords, filling interspaces between consecutive varices, and beginning at periphery of whorls.

Radula and anatomy unknown.

Table 1. Measurements of the type specimens of *Trophon parodizi* new species in mm.

Species	Length	Width	Whorls
T. parodizi			
Holotype	23	11	4
Paratype	21.1	10.6	4

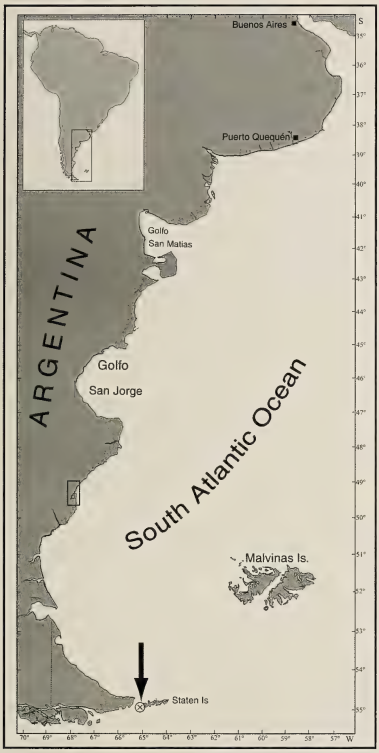


Figure 145. Map showing the type locality of *T. parodizi* new species (♦).

Type Material: 52°29′ S, 60°36′ W, West Falkland (Malvinas) Is., Svenska Sudpolar Expedition, 11 September 1902, Sta. 58, 197 m (NHRM 1041).

Additional Material Examined: 55°07′ S, 66°33′ W, 1 D, 83 m (MACN-In 23944-2).

Distribution: Around Malvinas Is. and the Magellanic region.

Remarks: "*Trophon*" *malvinarum* is a rare species known from only one specimen other than the holotype. It was originally described in the genus *Trophon*; however, the protoconch is somewhat shorter and symmetrical and the shell never develops true lamellae but low varices. It probably could be better assigned in the genus *Urosalpinx*. Assessment of its real affinities must wait until specimens with soft parts preserved can be studied.

CONCLUDING REMARKS

The geographic distribution of the species of the genus *Trophon* sensu stricto is restricted to the southwestern Atlantic and the southeastern Pacific Oceans. This distribution is certainly a consequence of their larval biology. Planktonic larval development is unknown to occur in the genus. Moreover, the larvae do not need to move any significant distance either for feeding or reproductive purposes—those from shallow water habitats live on mussel banks on which they feed and mate. Such a condition is reflected in the enormous morphological variation shown by the shells of the different species, particularly in *T. geversianus*. While most of the species are well known, some others were only collected in a single location (e.g., *T. amettei*) and therefore their range of variation remains to be known.

Radular and anatomical features suggest that the entire *Trophon* group from Patagonia is very homogeneous. All the species included in this genus have several common radular features. The most remarkable are: the intermediate denticle attached to the upper third of the internal edge of the lateral cusp of the rachidian teeth; a single marginal denticle in the external edge of the base of the rachidian teeth; the attachment area of the marginal teeth are always (no exceptions known) narrow, thin, with the free part of same thickness, and the central cusp of the rachidian is always thin and larger than the laterals (see also Pastorino, 2002).

The Antarctic species so far assigned to *Trophon* and the boreal ones recently included in the genus *Boreotrophon* (see Egorov, 1993) have the inner denticle between central and lateral cusp of the rachidian teeth always free, attached to the base of the teeth. In addition, most of the radulae of these northeastern Atlantic species—according to Bouchet and Warén's revision (1985)—have a broad attachment of the marginal teeth.

Conchological features are so variable that I considered them as secondary. However, the protoconchs are actually very different and allow for the division in at least two clearly defined groups. There is no ornamentation on the protoconchs of Patagonian representatives of *Trophon*, whereas most of the boreal species of *Boreotrophon* have a delicate pattern of irregular threads. The Antarctic species have also no ornamentation in the protoconch with only one exception: *T. scotianus* Powell, 1951 which has apparently the same pattern observed in North Atlantic *Boreotrophon* species.

There are several anatomical features that characterize the group of species living along the South American coast. The accessory salivary glands, when known, are usually tubular; the esophagus produces a typical esophageal loop after the valve of Leiblein and posteriorly runs appressed to the left side of the gland of Leiblein;

the esophageal glands in the mid-esophagus are inconspicuous, not externally visible; and finally, the penises are always dorso-ventrally flattened, with a large papilla and a simple *vas deferens* either closed by the overlapping sides of the penis or open.

The features mentioned above and the geological story of the two areas, Antartica and Patagonia, allow for the clear differentiation of these two groups.

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Latitudinal trends in shell characters of the neogastropod *Olivancillaria urceus* (Gastropoda: Olividae) in the temperate southwestern Atlantic Ocean

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ABSTRACT

Variation in shell characters of the neogastropod *Olivancillaria urceus* (Röding, 1798) was analyzed at the central part of its geographical range. Nine shell dimensions were measured from specimens from seven localities between 32°10′ S and 40°33′ S along the Atlantic coast of South America. Significant effects of collection site were detected on all measured variables. The first three components in principal component analysis together explained nearly 80% of the observed variance in morphometric measures. Variables also differ in their allometric trajectories among localities: all measured shell dimensions displayed both positive and negative allometric coefficients along the latitudinal axis. Allometric effects were then removed to allow for determination of size-free variation in shape. High-spired, elongated forms occurred more frequently in higher latitudes. Spire width, maximum width, maximum width/height and shell thickness decreased as latitude increased. Spire length measured on the apertural side showed an opposite trend. No relationship with latitude was found for fasciolar-band length and spire length (measured along the abapertural shell side). The existence of extreme forms within the analyzed sample showed high phenotypic and ecological plasticity in the populations assigned to *O. urceus*.

INTRODUCTION

Gastropod shell shape reflects a trade-off among functional requirements, energetics of construction and maintenance, rules governing growth, and the imprint of evolutionary ancestry. The result of the interactions between these factors on the realized shell is also affected by environmental features and tied to architectural constraints (Vermeij, 1993). Phenotypic plasticity in shell characters appears to exert a strong influence on small and large-scale morphological variation in marine snails (Trussel and Etter, 2001).

Different patterns in shell variation are found as different spatial scales and taxonomical or ecological hierarchies are considered: well-disseminated eco-geographical rules, suitable for many taxa, predict that animals at high latitudes should have larger body sizes and life spans than at low latitudes (Mayr, 1956; Atkinson and Sibly, 1997). In most mollusks growth is faster at high temperatures and in the presence of food than in cold, nutrient-poor conditions (Vermeij, 1993).

Latitudinal variation in shell characters was detected in northern hemisphere gastropods assemblages. This variability was related to efficiency of calcium carbonate utilization. It was shown that more heavily calcified and ornamented shells occur with decrease in latitude (Grauss, 1974).

When considering variation in shell features at the intraspecific level, it could be interpreted as a response to environmental conditions, which may include biotic and abiotic factors. Biotic interactions have been proposed as driving forces for morphological changes. Certain shell characters interpreted as anti-predatory features such as low spire and elongate aperture were found to be significantly different between comparable gastropod assemblages from both sides of the tropical Atlantic and Indo-West Pacific (Vermeij, 1978).

Within-location variation in shell shape and shore-level size gradients have been found for several species of intertidal mollusks (Vermeij, 1972). This intra-populational variability is often coupled with shifts in shell growth and has been related experimentally with food supply and density-dependant processes: specimens of *Littorina littorea* (Linnaeus, 1758) with plentiful supply of seaweed grow faster and develop low-spired shells than other group maintained under crowded conditions; in the latter growth was slower and higher spired shells were developed (Kemp and Bertness, 1984). De Wolf et al. (1998) documented large-scale patterns of shell variation in *Littorina striata*, a planktonic-developing periwinkle from Macaronesia, confirming expectations based

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Figure 1. Map showing parts of the Atlantic coast of Brazil, Uruguay, and Argentina that include the collection sites of *Olivancillaria urceus*.

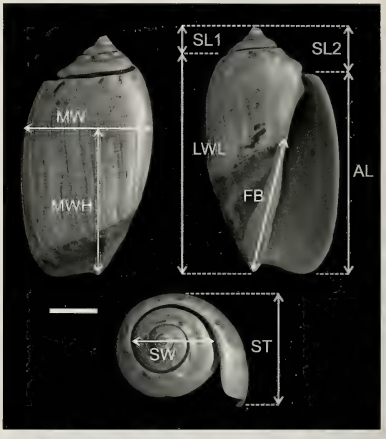

Figure 2. Dorsal, ventral, and apical view of *Olivancillaria urceus* showing measurements taken for statistical analysis. Scale bar = 1 cm. Abbreviations: LWL: last whorl length from suture to anterior end; AL: aperture length, distance along outer lip from suture to anterior end; FB: distance between anterior and posterior ends of fasciolar band along internal side of the aperture; MW: maximum linear distance from outer lip to opposite side; MWH: maximum linear distance perpendicular to MW to anterior end; ST: shell thickness; SW: diameter of spire base from tip of callus above aperture to opposite point on suture; SL2: lateral spire length from tip of callus above aperture to protoconch tip on outer lip side in ventral view, parallel to growth axis; and SL1: same length measured on the opposite side

on morphological patterns observed among other prosobranchs for increasing shell size and weight in southern sites.

There is also ontogenetic related variation due to allometric increase of spire length relative to other shell dimensions (Vermeij, 1993). In this context, remotion of allometric effects is needed in order to detect changes in shell shape.

However, most of the studies dealing with morphological variability in gastropods are restricted to intertidal rocky-shore snails, in particular those belonging to Littorinidae. We know of no attempt made to analyze or even describe patterns of intraspecific variation in neogastropod shell features along a latitudinal axis in the Southern Hemisphere.

The genus *Olivancillaria* d'Orbigny, 1839, is widely distributed along the Atlantic coast of South America. It comprises seven species occurring from tropical areas (Espírito Santo, Brazil) to temperate regions (Golfo San Matías, Argentina) (Burch and Burch, 1964; Klappenbach, 1964; 1965; 1966; Rios, 1994). *Olivancillaria urceus* (Röding, 1798) is distributed along the entire latitudinal range of the genus in subtidal soft bottoms, ranging from the surf zone to at least 35 m depth (Juanicó and Rodríguez-Moyano, 1976; Milstein et al., 1976; Escofet et al., 1979; Scarabino, 1984) and exhibiting conspicuous differences in shell shape as noticed by Baratinni and Ureta (1961). For these reasons, this species is suitable for the examination of patterns of morphological variation in the region.

In this paper we document large-scale variability in shell features of *Olivancillaria urceus* in the temperate sector of it distribution range and analyze this species variability along the latitudinal axis. We also discuss possible ecological implications of the observed pattern.

MATERIALS AND METHODS

A total of 193 specimens collected in seven sites between 32° and 40° S along the Atlantic coast of South America were analyzed. Collection sites were Cassino Beach, Brazil (32°10′ S, 52°20′ W, Site 1), La Coronilla (33° 57′ S, 53°30′, Site 2), La Paloma (34°38′ S, 54°08′ W, Site 3) and Punta del Este (34°36′ S, W 55° 18′ W, Site 4), Uruguay, and Mar del Plata (38°02′ S, 57° 32′ W, Sites 5), Puerto Militar (38°44′ S, 62°10′ W, Site 6) and San Antonio Oeste (40°33′ S, 64°50′ W, Site 7), Argentina (Figure 1). Examined material is deposited at Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina) and Museo Nacional de Historia Natural (Montevideo, Uruguay).

Nine shell dimensions were measured with vernier

Table 1. Sample size, % of variation accounted by PC1 and allometric coefficients for morphometric variables in each collection site. Abbreviations: LWL: last whorl length from suture to anterior end; AL: aperture length, distance along outer lip from suture to anterior end; FB: distance between anterior and posterior ends of fasciolar band along internal side of the aperture; MW: maximum linear distance from outer lip to opposite side; MWH: maximum linear distance perpendicular to MW to anterior end; ST: shell thickness; SW: diameter of spire base from tip of callus above aperture to opposite point on suture; SL2: lateral spire length from tip of callus above aperture to protoconch tip on outer lip side in ventral view, parallel to growth axis; and SL1: same length measured on the opposite side.

Variable	Locality						
	1	2	3	4	5	6	7
Sample size	27	17	39	18	43	21	28
% of variation accounted for by PC1	65.33	67.54	84.36	71.81	94.23	87.82	75.44
Allometric coefficients							
LWL	1.258	0.492	1.098	1.144	1.063	0.985	0.890
AL	1.451	0.374	1.166	0.965	1.072	1.028	1.125
FB	1.544	0.617	1.207	1.086	1.142	1.05	0.948
MW	1.101	0.382	1.12	1.089	1.102	1.134	1.123
MWH	1.386	0.459	1.163	1.041	1.134	1.026	1.062
ST	1.214	0.485	1.143	1.159	1.118	1.043	1.151
SW	1.294	0.760	1.338	1.101	1.136	1.165	1.285
SL1	0.025	2.573	0.426	0.619	0.623	0.750	0.765
SL2	−0.274	2.858	0.340	0.796	0.610	0.819	0.650

calliper, within an accuracy of 0.05 mm. Abbreviations for the variables are as follows: LWL: last whorl length from suture to anterior end; AL: aperture length, distance along outer lip from suture to anterior end; FB: distance between anterior and posterior ends of fasciolar band along internal side of the aperture; MW: maximum linear distance from outer lip to opposite side; MWH: maximum linear distance perpendicular to MW to anterior end; ST: shell thickness; SW: diameter of spire base from tip of callus above aperture to opposite point on suture; SL2: lateral spire length from tip of callus above aperture to protoconch tip on outer lip side in ventral view, parallel to growth axis; and SL1: same length measured on the opposite side (Figure 2). Collection sites were grouped *a priori* for discrimination of differences among samples from different geographic regions. For this we used the non-parametric Kruskall-Wallis ANOVA median test. Allometric coefficients for the seven collection sites were calculated for all variables. The method used was based on Jolicoeur (1963) with additions from Kowalewski et al. (1997). Data were log-transformed and subjected to principal component analysis (PCA). The first principal component (PC1) was regarded as a size axis. Correlation between sampling size and explained variance was examined by means of regression analysis. The allometric coefficient for each original variable was estimated by dividing the PC1 loading for that variable by the mean PC1 loading over all variables. Estimation of 95% confidence intervals for the allometric coefficients was made by bootstrapping specimens (2000 bootstrap replicates were made, not shown).

Size effects were then removed, following Lleonart et al. (2000), by scaling all individual to the same size (mean LWL) adjusting their shape to the one they would have in the new size according to allometric change. PCA was run on transformed data and loads of the eight remaining variables (i.e., all but total length) were calculated. This removal method is one of the most powerful tools available, since it is in turn a theoretical generalization of the technique used by Thorpe (1975, 1976), which was recorded as one of the most efficient methods in the empirical evaluation done by Reist (1985).

A cluster analysis (single linkage, Euclidean distances) was then performed to discriminate among possible morphological groups using site mean value for each variable. The cophenetic correlation coefficient (CCC) was calculated to measure the internal distortion of the cluster analysis following Sokal and Rolf (1962). Finally, possible relationships between latitude and shell characters were examined by regression analysis.

RESULTS

All variables showed significant differences between sites (non–parametric ANOVA: $p < 0.01$). PCA performed with log-transformed data showed that variance explained by PC1 (Factor 1, regarded as size axis) differed among sampling sites and varied between 65.33% (site 1) and 94.23% (site 5). Explained variance was not correlated with sample size (regression analysis, $F = :0.010$, p-level = 0.922). Allometric coefficients calculated for the nine variables also varied among collection sites. All variables displayed both positive ($b > 1$) and negative ($b < 1$) allometric trajectories (Table 1).

The first three factors in size-free PCA explained together 79.38% of the total variance. Variables MW, MHW, ST, and SW grouped together with positive loads on Factor 1. SL1 and SL2 formed another highly cor-

Table 2. Results of size-free PCA Analysis. % of variance accounted by each factor and loading of each variable are shown. Abbreviations: LWL: last whorl length from suture to anterior end; AL: aperture length, distance along outer lip from suture to anterior end; FB: distance between anterior and posterior ends of fasciolar band along internal side of the aperture; MW: maximum linear distance from outer lip to opposite side; MWH: maximum linear distance perpendicular to MW to anterior end; ST: shell thickness; SW: diameter of spire base from tip of callus above aperture to opposite point on suture; SL2: lateral spire length from tip of callus above aperture to protoconch tip on outer lip side in ventral view, parallel to growth axis; and SL1: same length measured on the opposite side.

	Factor loadings		
Variable	PC1	PC2	PC3
% of variation	41.54	22.9	14.95
AL	0.422	−0.474	0.550
FB	0.173	−0.487	0.716
MW	0.874	0.2125	−0.063
MHW	0.888	0.083	0.034
ST	0.858	0.226	−0.111
SW	0.811	0.246	−0.044
SL1	−0.094	0.815	0.446
SL2	−0.396	0.735	0.399

related group loading positively on Factor 2, and AL and FB did the same on Factor 3 (Table 2).

Two different groups were discriminated when the collection-site mean value for each variable were plotted onto a hierarchical cluster, one of these groups composed by individuals belonging to sites 6 and 7 (Figure 3). The calculated value for CCC was 0.93.

Latitudinal-related patterns of variation were found in variables MW, MHW, ST, AL, and SW. This group of variables showed a decreasing trend with increasing latitude. On the other hand, SL2 tend to increase with latitude, whereas SL1 and FB displayed no relationships. The coefficient of determination (r^2) explained less than 30% for all variables (Figure 4).

DISCUSSION

The present work documents shell shape variation in *O. urceus* along a latitudinal gradient. The results show that shell features vary between sites. The analyses presented above show that northern forms are stunt, low-spired, and conical, whereas southern specimens (mostly those from sites 6 and 7) are high-spired, narrower and elongated.

Within location variation may be due to local differences in habitat conditions, for example, contrasting beach morphodynamics, which are in turn associated with different sediment features. However, the poor geographical definition of collection sites did not allow us to assign in all cases a particular individual to a particular habitat. Notwithstanding, intraspecific phenotypic plasticity in a small spatial scale is known to occur in mollusks. For example, observations made on the muricid *Nucella lapillus* (Linnaeus, 1758) showed that specimens from very exposed shores are short-spired when compared with those from sheltered localities (Cooke, 1895; 1915).

When considering variation at a geographic scale, two possible scenarios are suggested to explain the among-collection sites differences. These are either: (1) a gradual response to shifts in environmental conditions along the latitudinal gradient that generate a shape gradient (in this scenario, macro-scale variation in physical parameters such as sea water temperature and calcium carbonate availability could be correlated with the observed variation); or (2) different morphs associated with par-

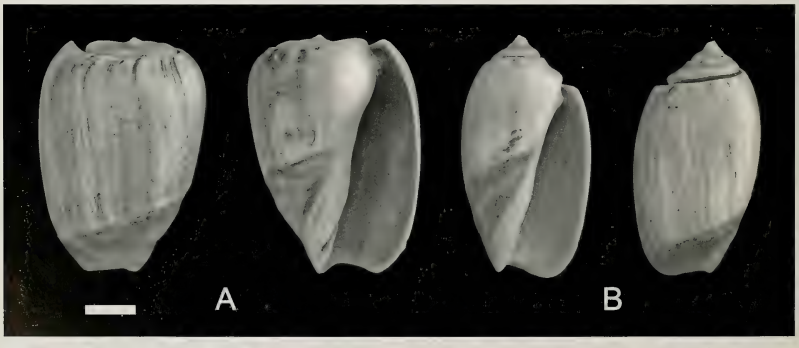

Figure 3. Extreme forms of *Olivancillaria urceus* in the study area. **A.** dorsal and apertural view of specimens from site 3. **B.** Dorsal and apertural views of specimens from site 7. Scale bar = 1 cm

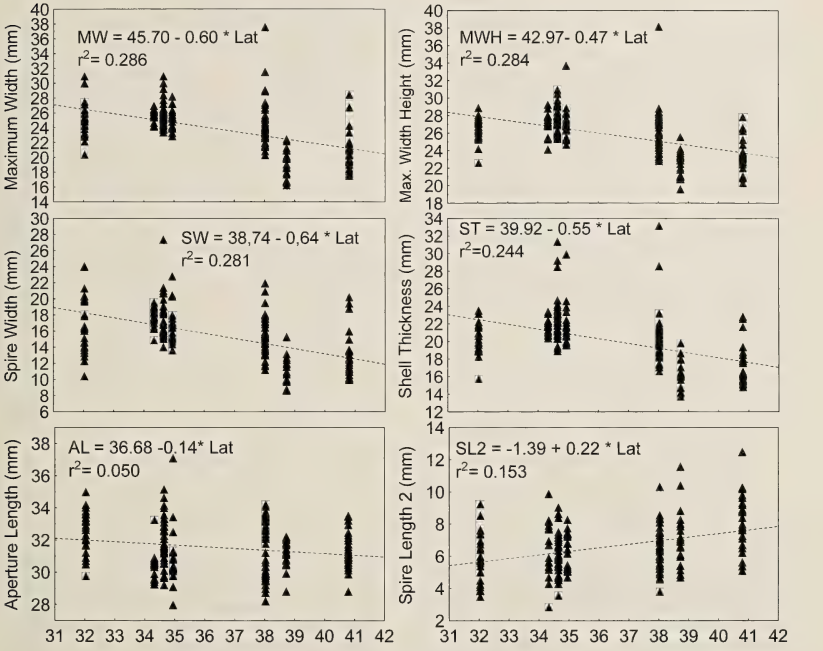

Figure 4. *Olivancillaria urceus*, relationship between standardized shell characters and latitude. Coefficients of determination (r^2) and linear model fitted are shown.

ticular habitats, such as exposed sandy beaches or sheltered bays: broader specimens with short spire in high-energy habitats and high-spired, elongated forms in protected habitats. In this case, likelihood of occurrence of one particular morph depends on environmental characteristics of geographic locations and may be considered local populational phenomena.

A related species, *Olivancillaria vesica* (Gmelin, 1791) also shows two geographical forms, recognized as subspecies, which are easily separable along its distribution range (Klappenbach, 1966). This species shows an opposite latitudinal pattern: northern forms are narrower and longer compared with the broader, "auriculated" (ear-shaped) southern forms. In accordance with (2), the latter form extends along the southern coast of Brazil (Santa Catarina), Uruguay, and Argentina as far as Puerto Quequén, Province of Buenos Aires, the same geographical area in which *O. urceus* displays broader and low spired shells. These broader shell forms could be interpreted as associated with a large foot that enhances its ability of "anchoring" to the substratum in higher energy environments, thus improving individual fitness. However, more study is necessary on the taxonomic status on *O. vesica* forms before any analysis of its morphological variation.

It can be argued that differences in spire length and width reflect shifts in growth patterns associated with the adaptive process. It should be noticed that there is a coincidence between occurrences of high-spired forms (associated with slower growth mode) in higher lati-

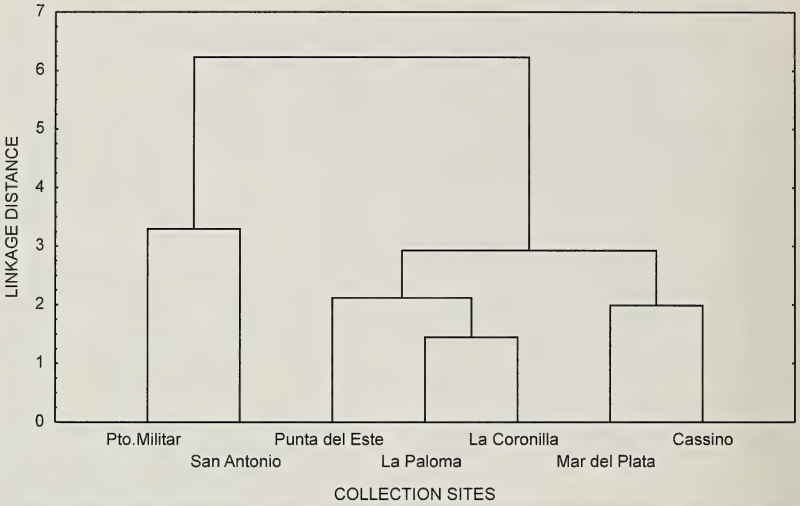

Figure 5. *Olivancillaria urceus,* cluster analysis. Collection sites were grouped on the basis of similarities in the mean value for each morphometric variable.

tudes. This could be supporting the hypothesis that both latitudinal and environmental effects may be coupled together in a combined effect that masks the isolated effects of each factor.

As demonstrated by PCA analysis, nearly half of the variance is explained by PC1 (42% of total variance), which in turn is mainly affected by MW, MWH, ST, and SW. This fact implies that changes in shell shape detected within the analyzed sample are due mostly to differences in its variables. Variation observed in SL2 and SL1 are of much less importance as form determinants when considering total variance components. However, height and shape of the spire and protoconch characters have been regarded as important specific (López et al., 1988) and supraespecific (Tursch, 1988) features, for which these characters deserves further analysis. Nevertheless, it seems that macrogeographic variation in shell morphology strongly depend on local conditions, which make adequate sampling and data treatment very difficult.

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Errata

Due to an editorial lapse, the Introduction section was omitted from Köhler and Glaubrecht's (2005) article in the most recent issue of The Nautilus. The missing Introduction is printed below (literature references are in the main article), with apologies to the authors and readers.

Fallen into oblivion—the systematic affinities of the enigmatic *Sulcospira* Troschel, 1858 (Cerithioidea: Pachychilidae), a genus of viviparous freshwater gastropods from Java

Frank Köhler
Matthias Glaubrecht

INTRODUCTION

The first volume of the well-known work *"Das Gebiss der Schnecken zur Begründung einer natürlichen Klassifikation"* ['Establishing a natural classification of snails from their dentition'] by Franz Hermann Troschel (1810–1882) was published in parts between 1856 and 1863. The work is an important historic landmark in the enduring challenge of zoologists to create a natural classification of the living gastropods. In his work, Troschel (p. 117) described the genus *Sulcospira* within the tribus 'Pachychili' mainly based on features of the operculum and the radula (Figure 1). According to Robertson (1957), that description was published in 1858. Within the non-marine Cerithioidea, *Sulcospira* represents one of the least known genera of Southeast Asian Pachychilidae, a group of viviparous freshwater gastropods we have been focusing on in the last few years.

Recent research aiming to propose a phylogenetic systematics hypothesis and to establish a natural classification of this limnic gastropod family will also allow a better understanding of their evolution, morphology, and ecology (Glaubrecht, 1996; 1999; Köhler and Glaubrecht, 2001; 2002; 2003; Glaubrecht and Rintelen, 2003). Only recently, the Pachychilidae Troschel, 1857, have been shown to represent a monophyletic group clearly distinct from the Thiaridae Troschel, 1857, and from the other limnic Cerithioidea. This new concept has been suggested by analyses of morphological data (e.g. Glaubrecht, 1996; 1999) and is corroborated by molecular data suggesting that Thiaridae (e.g. *Melanoides*, *Thiara*, *Tarebia*) and Pachychilidae (e.g. *Paracrostoma* Cossmann, 1900, *Pachychilus* Lea, 1850) are not very closely related to each other (see phylogenetic reconstruction in Lydeard et al., 2002: figs. 1, 2). This classification conflicts with the traditional view of most earlier authors who treated pachychilid taxa as 'Melaniidae' = Thiaridae (among others, Thiele, 1929; Rensch, 1934; Benthem-Jutting, 1956; Brandt, 1968; 1974) or Pleuroceridae (e.g. Ponder and Warén, 1988; Vaught, 1989).

However, our current knowledge of the phylogeny and systematics of freshwater Cerithioidea in general and the Pachychilidae in particular is still limited, since many taxa remain poorly known. Only recently, systematic studies using morphological as well as molecular genetic data have shed some light on the relationships of several other genera within the Pachychilidae. For instance, Köhler and Glaubrecht (2001) presented comparative morphological data on taxa traditionally assigned to *Brotia* H. Adams, 1866, by various authors, revealing that this genus as previously perceived actually comprises four lineages, each characterized most conspicuously by distinct reproductive morphologies.

Subsequent studies including molecular phylogenetics data put special emphasis on two of these lineages, *Jagora* Köhler and Glaubrecht, 2003, endemic to the Philippines (Köhler and Glaubrecht, 2003) and *Tylomelania* F. and P. Sarasin, 1898, endemic to Sulawesi (Rintelen and Glaubrecht, 1999; 2003), suggesting an independent generic status for each. In addition, the properties of another Australasian pachychilid genus, *Pseudopotamis* Martens, 1894, have been extensively described by Glaubrecht and Rintelen (2003). Hence, a notable portion of crucial biological information on pachychilids has been amassed, helping to facilitate a better understanding of pachychilid systematics, phylogeny, and evolution.

Nevertheless, there remain a number of systematic and taxonomic problems and difficulties related to this group of freshwater snails. One of them will be dealt with in this study: The taxonomy and systematic position of *Sulcospira*.

Among the various generic names that have been introduced for Southeast Asian pachychilid taxa, *Sulcospira* is clearly the oldest one. Its description predates that of other names, such as *Brotia*, *Antimelania* Fischer and Crosse, 1892, or *Pseudopotamis*; a complete annotated list of the introduced supraspecific names within the Southeast Asian Pachychilidae is given in Köhler and Glaubrecht (2002). Consequently, every other supraspecific pachychilid taxon is valid only with the reserve that it is not a junior synonym of *Sulcospira*. In spite of this significant taxonomic role of *Sulcospira*, this taxon has been widely ignored, especially by modern systematists. Thus, another aim of this article is to compile all available information on *Sulcospira* and to provide new data from our own examinations of the limited

material from museum collections. In addition, implications for pachychilid taxonomy and systematics are discussed in relation to *Sulcospira*.

LITERATURE CITED

Köhler, F. and M. Glaubrecht. 2005. Fallen into oblivion—the systematic affinities of the enigmatic *Sulcospira* Troschel, 1858 (Cerithioidea: Pachychilidae), a genus of viviparous freshwater gastropod from Java. The Nautilus 119: 15–26.

In the recently published article by Ardila and Valdés (2004), please note the following corrections:

On page 134, caption of Figure 3, replace "*Armina muelleri* Thompson, Cattaneo and Wong, 1990", for "*Armina muelleri* (Ihering, 1886)";

On the same page, the adjacent subsections "**Type Material**" and "**Type Locality**" should be replaced by:

Material Examined: MHNMC INV MOL3901, 32 mm length, alive, from off Salamanca Island, Colombia (11°5′46″ N, 74°40′35″ W), 20 m depth, hard bottom with pennatulaceans (*Renilla reniformis* and *Renilla muelleri*).

LITERATURE CITED

Ardila, N. E. and A. Valdés. 2004. The genus *Armina* (Gastropoda: Nudibranchia: Arminidae) in the southern Caribbean, with the description of a new species. The Nautilus 118: 131–138.

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CONTENTS

Cristián Ituarte — The Sphaeriidae (Bivalvia) from northwestern Argentina including three new species of *Pisidium* 93

Shannon M. Carpenter — *Mysella pedroana*, a commensal bivalve (Lasaeidae) on two decapod crustacean hosts 105

Paolo Mariottini
Carlo Smriglio
Emilio Rolán — *Coralliophila trigoi* (Gastropoda: Muricidae), a new species from the northeastern Atlantic Ocean 109

Book Review 116

The Sphaeriidae (Bivalvia) from northwestern Argentina including three new species of *Pisidium*

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ABSTRACT

Knowledge on the Sphaeriidae fauna in southern South America is significantly improved with the description of three new species of the genus *Pisidium* from Salta and Jujuy provinces (northwestern Argentina). This paper provides the first record of sphaeriids in restrictive high-altitude South American environments, particularly from very small water courses found in "vegas", exceptionally localized areas of "cushion vegetation" or "cushion peat bogs" developing between 2000–4000 m altitude in the Argentine pre-Andean ranges. Furthermore, the geographic distribution range of *Pisidium chiquitanum* Ituarte, 2001, only reported to date from the type locality in sub-Andean regions of central Bolivia, is considerably enlarged.

INTRODUCTION

The Sphaeriidae fauna from Argentina is poorly known; the first reports were those by Strobel (1874) on *Musculium argentinum* (d'Orbigny, 1835) and Pilsbry (1911) describing several new species of *Pisidium* C. Pfeiffer, 1821, and *Musculium* Link, 1807, from Patagonia. Later on, Doello-Jurado (1921) described the first species of *Eupera* Bourguignat, 1854, from Argentina, and Ituarte (1989, 1994) and Ituarte and Dreher-Mansur (1993) described three new species of *Eupera* from Iguazú, Uruguay and Paraná River basins in northeastern Argentina. Regarding the species diversity of *Pisidium* C. Pfeiffer, 1821, twelve species are known from Patagonia and Northeastern provinces (Ituarte, 1996, 1999, 2000).

Only two species of Sphaeriidae have been reported from northwestern Argentina: *Sphaerium lauricochae* (Philippi, 1869), from Jujuy Province (Ituarte, 1995) and *Musculium argentinum* from Mendoza Province (Strobel, 1874). The species diversity of *Pisidium* has essentially not been documented. In the present paper, three new species of *Pisidium* from lowland and high-altitude habitats in the pre-Andean mountain ridges are described. Based on new findings the knowledge on the geographic distribution of *Pisidium chiquitanum* Ituarte, 2001, is updated.

MATERIALS AND METHODS

Materials for the present study were obtained during three field trips to Northwestern Argentina (Tucumán and Salta provinces in March 1999, Salta and Jujuy provinces in December 2001 and March 2004, and Catamarca Province in March 2004). Figure 1 shows the location of collecting sites; more detailed information on the source of specimens is given in the Systematics section. The collected specimens were fixed immediately after collecting in 70° alcohol after being relaxed through a short rinse (around 20 seconds) in warm water (about 50°C). Specimens for scanning electron microscopy (SEM) were cleaned by repeated rinsing in distilled water followed by a short treatment (about 5 seconds) in 10% sodium hypochlorite solution. Soft anatomy was studied after decalcification of valves through a 12-hour rinsing in a 5% formaldehyde and 2% acetic acid solution. Linear measurements (shell length [SL], shell height [SH], shell width [SW] and presiphonal suture length [PSS]), shape indices and morphometric ratios (height index [HI= SH/SL], convexity index [Ci= SW/SH], ratio of hinge length [HiL] to shell length [HiL/SL]), were calculated according to the criteria followed by Ituarte (1996). For each calculation (n= 10, unless otherwise stated), mean and standard deviation values are given.

Type specimens are deposited at Museo de La Plata, La Plata (MLP), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN), Fundación Miguel Lillo, Tucumán (FML) and Muséum National d'Histoire Naturelle, Paris (MNHN). Types of *Pisidium chiquitanum*, housed at Museo de Historia Natural "Noel Kempff Mercado", Santa Cruz de La Sierra, Bolivia (MHNB) and MLP were also used for comparative purposes.

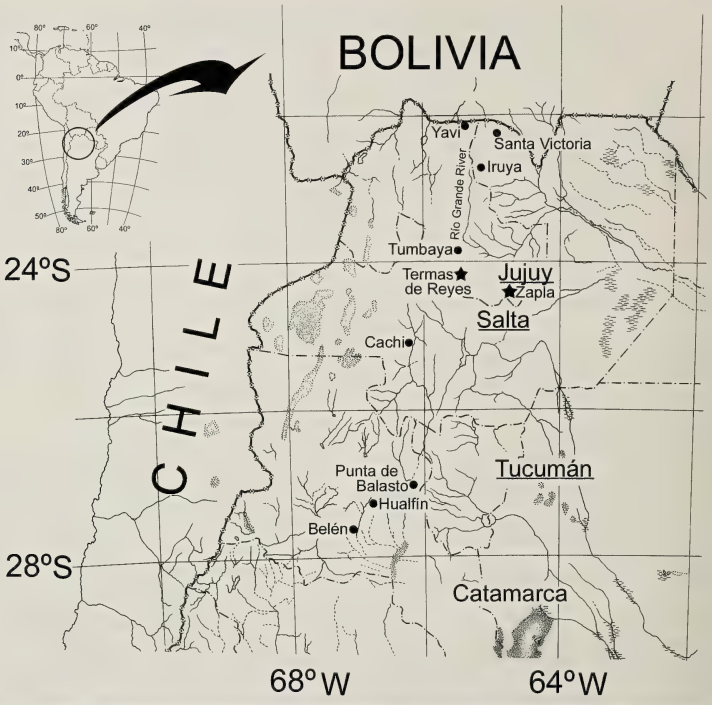


Figure 1. Location map. Stars in black indicate type localities of *Pisidium omaguaca* new species, *Pisidium ocloya* new species, and *Pisidium chicha* new species.

SYSTEMATICS

Pisidium omaguaca new species
(Figures 2–15)

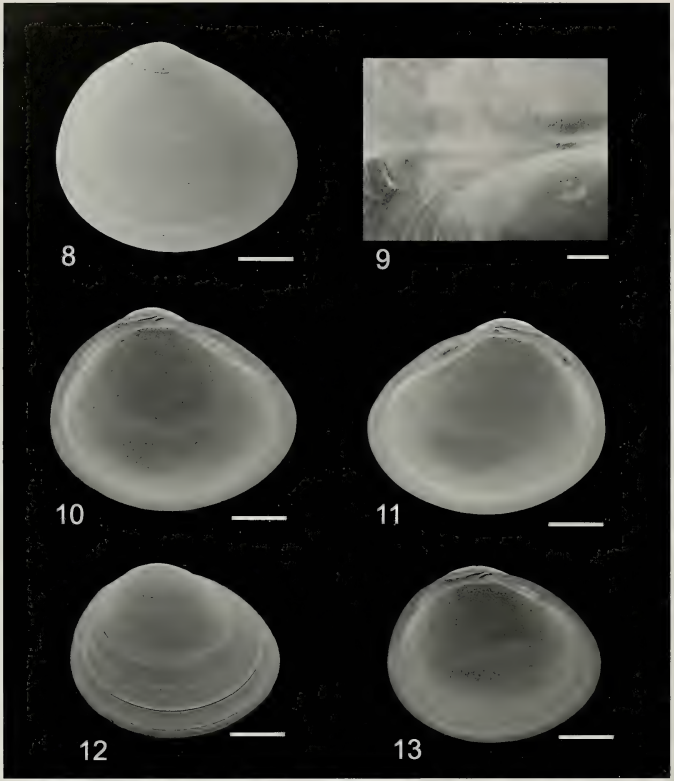
Diagnosis: Shell markedly oval, high and anteriorly produced, beaks depressed, displaced backward, not projecting from shell surface and only barely visible above dorsal margin; ligament internal; anal and branchial mantle openings present; two demibranchs present, nephridia of closed type, with lateral lobe not visible in lateral or dorsal views.

Description: Shell thin, translucent, small to medium size (mean SL = 2.73 ± 0.17, maximum observed size: 3.7 mm), rather high (mean HI = 85 ± 1) (Figure 2), not inflated (mean Ci = 58 ± 3) (Figures 2, 3). Shell outline markedly oval, anteriorly elongated. Anterior end produced in a sharp curve, posterior end short, widely rounded, sometimes slightly truncated and straight (Figures 2, 4, 5, 8). Dorsal margin short, weakly connected with anterior margin, which slopes markedly towards anterior end; sometimes, a gentle angle marks joining point of dorsal and posterior margins (Figure 8). Beaks very low, depressed and wide, not raised from shell surface, only slightly projected above dorsal margin, displaced backward, located at about 59% of SL (Figures 2, 4, 5). Shell surface finely and somewhat irregularly striated, glossy, amber.

Hinge plate strong, hinge line short (HiL/SL = 53 ± 3), strongly curved. Hinge: Left valve (Figures 4, 6): cardinal teeth well-developed, the inner one (C_2) thin, short at base, bent upward, slightly oblique with respect

Figures 2–7. *Pisidium omaguaca* from Termas de Reyes, Jujuy. **2.** Holotype (MLP 5496-1-1): outer view of right valve. **3–7.** Paratypes (MLP 5496-1-2). **3.** Posterior view. **4.** Left valve, inner view. **5.** Right valve, inner view. **6.** Left valve, detail of hinge. **7.** Right valve, detail of hinge. Scale bars = 500 μm.

to antero-posterior axis, rounded at the tip, outer cardinal tooth (C_4) a narrow, slightly wider at posterior end, uniformly curved blade, quite oblique, overlapping C_3 at posterior half; anterior lateral tooth (AII) very strong, short, nearly straight, cusp high, pointed, displaced forward; posterior lateral tooth (PII) minute, straight and strong, cusp high, distally displaced. Right valve (Figures 5, 7): cardinal tooth (C_3) not strong, somewhat displaced forward, curved in the middle, quite narrow at anterior half, slightly enlarged in a posterior,

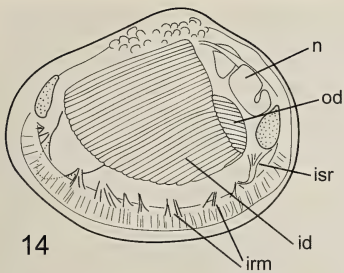


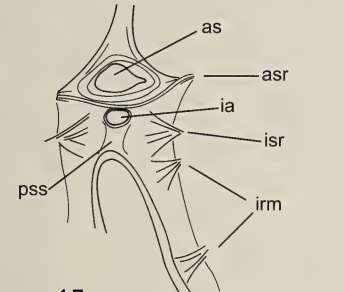
Figures 8–13. *Pisidium omaguaca*. **8.** Paratype (MLP 5485). Right valve, outer view. **9.** Paratype (MLP 5496-1-2). Dorsal view, detail of the escutcheon. **10–11.** Inner view of left and right valves of a specimen from Tiraxi, Jujuy (MLP 6535). **12, 13.** Outer and inner views of right and left valves of a specimen from a "peat bog" between Yavi (Salta) and Santa Victoria (Jujuy) (MLP6559). Scale bars (**8, 10–13**) = 1000 µm; (**9**) = 200 µm.

elongated cup. Lateral teeth short and robust, inner anterior lateral (AI) curved, cusp subcentral or slightly displaced anteriorly; outer anterior lateral tooth (AIII) quite short, cusp distal; inner posterior lateral (PI) nearly straight, short, cusp subcentral; outer posterior lateral (PIII) minute, with distal cusp.

Ligament-pit enclosed, deep, inner margin straight or slightly concave (Figures 6, 7). Ligament relatively short, representing 20 ± 1% of shell length, strong, internal, never visible from outside (Figure 9). Escutcheon inconspicuous (Figure 9).

Anatomy: Anal siphon and branchial inhalant mantle opening present. Presiphonal suture about 9% of shell length (Figure 15). Eight or nine well-marked muscle scars located away from pallial line correspond to inner radial mantle muscles. Muscle scars corresponding to anal siphon retractors are coalescent with that of





Figures 14–15. *Pisidium omaguaca* new species. **14.** Gross anatomy. **15.** Mantle muscles. (**as:** anal siphon; **asr:** anal siphon retractor; **ia:** inhalant aperture; **id:** inner demibranch; **isr:** inhalant siphon retractor; **irm:** inner radial mantle muscles; **n:** nephridium; **od:** outer demibranch; **pss:** presiphonal suture).

posterior adductor muscle (Figures 4, 5). Bundles of fibers of inner radial mantle muscles strong, converging anteriorly, except for two posterior bundles (Figures 4, 5, 14).

Inner and outer demibranchs present. Outer demibranch much smaller, formed by 10–12 very short descending filaments, reaching back to the 14th filament of inner demibranch (Figure 14). Up to three large embryos (1.3 mm length) were found within each brood pouch of a specimen 3.7 mm L. Nephridia of closed type, dorsal lobe, usually subquadrate, completely covering pericardial part of nephridium (Figure 14).

Type Locality: A small watercourse opening into Reyes River at Termas de Reyes, 24°10′19″ S, 65°29′27″ W, 1754 m altitude, Jujuy Province, Argentina (Figure 1).

Type Material: Holotype (MLP 5496-1-1) and 42 paratypes from the type locality (16 paratypes MLP 5496-1-2; 6 paratypes MLP 5485; 4 paratypes MACN-In 36361; 12 paratypes FML 14506; and 4 paratypes MNHN.

Other Material Examined: Jujuy Province: numerous specimens from the type locality (MLP 5496-1-3); Tumbaya, small pool with vegetations at the side of national road No. 9 (23°47′28″ S, 65°28′37″ W), 2070 m (MLP 6548); small stream flooding from springs in highland areas covered with "cushion vegetation", between Yavi (Jujuy) and Santa Victoria (Salta) (22°07′11″ S 65°13′05″ W), 4150 m (MLP 6559); small pool at the side of Río Grande River (22°58′14″ S 65°27′01″ W), 3950 m (MLP 6530); small springs at side of Manzanito Rivulet, near Huertas (22°14′20″ S 65°00′31″ W), 2740 m (MLP6551); small stream at the side of the road to Yala (24°07′20″ S 65°24′16″ W), 1430 m (MLP 6531). Salta Province: unnamed brook on provincial road No. 57, near Cachi (25°05′24″ S 66°07′33″ W), 2340 m (MLP 6540).

Distribution: Highlands of Jujuy and Salta provinces, Argentina, between 1400 and 4100 m altitude.

Etymology: The name refers to the Omaguacas, ancient aboriginal inhabitants of the Quebrada de Humahuaca, the spectacular 150 km long valley of the Río Grande River (Figure 1), which underwent a major cultural change during the past 10,000 years.

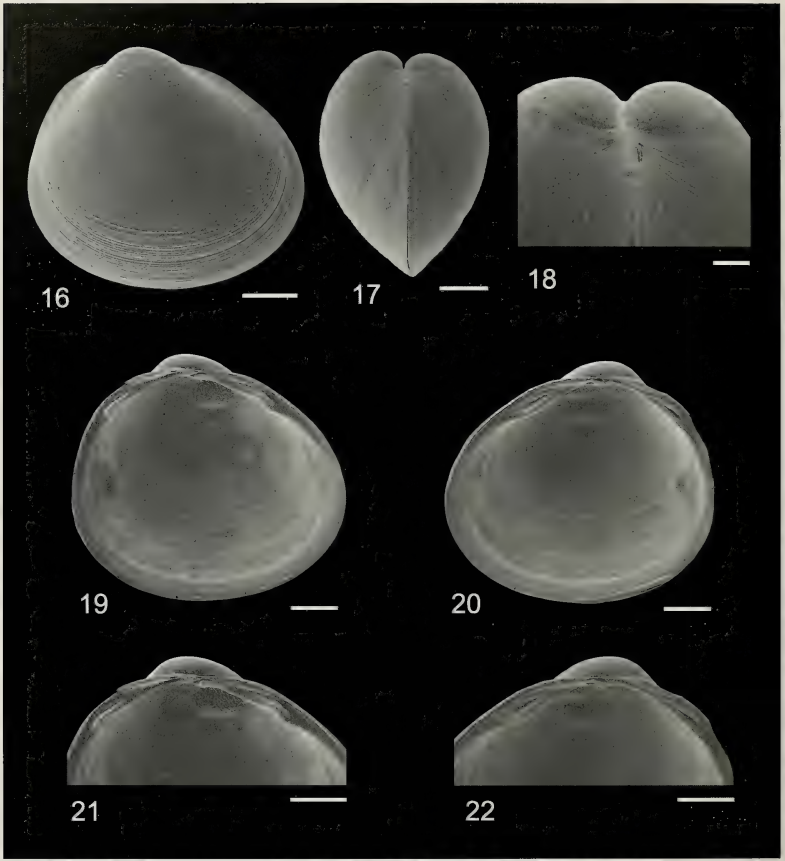
Remarks: *Pisidium omaguaca* new species differs from *Pisidium meierbrooki* Kuiper and Hinz, 1984, in being higher and less obese, having lower and not inflated beaks, and a more broadly rounded posterior end. *Pisidium omaguaca* new species is similar to *Pisidium chiquitanum* Ituarte, 2001, in soft anatomy, but differs in having a more solid and higher shell, with posterior end shorter and anterior half of dorsal margin sloping markedly towards the anterior end.

Pisidium ocloya new species
(Figures 16–33)

Diagnosis: Shell rather trapezoidal and high, small size, presence of only one (anal) mantle aperture and one demibranch.

Description: Shell thin, translucent, of small to medium size (maximum observed SL = 3.2 mm), high (mean HI = 85 ± 2), quite convex (mean Ci = 77 ± 4), shell outline rather trapezoidal. Anterior end somewhat produced in a sharp curve, posterior end short, truncate, somewhat oblique (Figures 16, 17). Beaks full, wide at base, markedly raised from shell surface and projected above dorsal margin, subcentral or slightly displaced backward, located at about 58% of SL (Figures 16, 19, 20). Shell surface finely and irregularly striated (Figures 16, 18), glossy, whitish or yellowish.

Hinge plate not strong, narrow in middle, hinge line rather long (HiL/SL = 56 ± 2), arcuate. Hinge on right valve (Figures 20, 22): cardinal tooth (C_3) delicate,



Figures 16–22. *Pisidium ocloya* new species from Burrumayo River, Jujuy. **16.** Holotype (MLP 5499-1): outer view of right valve. **17–22.** Paratypes (MLP 5499-2). **17.** Posterior view. **18.** Posterior view, detail of ligament. **19.** Left valve, inner view. **20.** Right valve, inner view. **21.** Left valve, detail of hinge. **22.** Right valve, detail of hinge. Scale bars (**16, 17, 19–22**) = 500 μm; (**18**) = 200 μm.

rather weak, slightly curved, narrow on anterior half, enlarged into a well-marked, blunt, posterior cup. Lateral teeth robust, inner anterior lateral (AI) well-developed, cusp displaced distally; outer anterior lateral tooth (AIII) shorter and weaker, cusp distal; inner posterior lateral (PI) gently curved, not long, cusp distally displaced; outer posterior lateral (PIII) reduced in size, with distal cusp. Hinge on left valve (Figures 19, 21): cardinal teeth minute, inner one (C_2) short and high, horizontal with respect to antero-posterior axis,

outer one (C_4) short, oblique, slightly overlapping C_2 at posterior end; anterior lateral tooth (AII) very strong, cusp high, distal; posterior lateral tooth (PII) shorter and weaker, cusp high, distal.

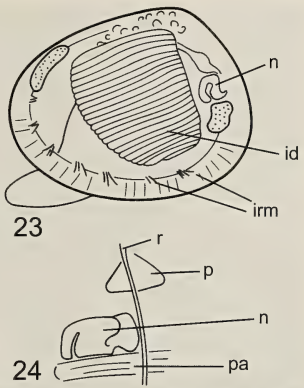
Ligament-pit enclosed, deep, inner margin slightly and evenly curved (Figures 21, 22), Ligament narrow, relatively long, representing 24 ± 1% of shell length, visible from outside and somewhat protruded at anterior half of ligament length. Escutcheon slightly marked by a delicate lanceolate line (Figures 17, 18).

ANATOMY: Only one demibranch (inner) present (Figure 23). Only anal mantle opening present. Inner radial mantle muscles weak, 6–7 bundles of few weak fibers converging anteriorly, attached just above pallial line (Figure 23); sometimes scars corresponding to inner radial muscles coalescent with pallial line (Figures 19, 20). Anal siphon retractors attached immediately ventrally to posterior adductor muscle. Nephridium with lateral loop visible dorsally (Figure 24).

Type Locality: Small flooded areas on the banks of Burrumayo River (24°10′18″ S, 65°22′43″ W), 1201 m altitude, in the neighborhood of Jujuy City, Jujuy Province, Argentina; and unnamed brook opening into Zapla River (24°16′03″ S, 65°07′09″ W), 946 m altitude, Zapla, Jujuy Province, Argentina.

Type Material: Holotype (MLP 5499-1) and 15 paratypes from the outskirts of Jujuy City (6 paratypes MLP 5499-2; 10 paratypes FML 14505; 56 paratypes from Zapla (36 paratypes MLP 6899-2; 10 paratypes MACN-In 36362; 10 paratypes MNHN).

Other Material Examined: Catamarca Province: unnamed brook at national road No. 40 at La Ciénaga de Abajo, between La Ciénaga and Belén (27°31′05″ S, 66°59′08″ W), 1520 m (MLP 7201); Jujuy Province: numerous specimens from the type locality (MLP 7369); unnamed brook on side of provincial road No. 4 at Guerrero (24°11′13″ S, 65°26′51″ W), 1650 m (MLP 7379); small spring on side of provincial road No. 4, near Termas de Reyes (24°10′36″ S 65°28′18″ W), 1730 m (MLP 5497-1, MLP 7370-1); small water course on side of national road No. 9 at Tumbaya (23°51′26″ S, 65°27′57″ W), 2020 m; Los Cedros Rivulet, south to "El Carmen" (24°28′0″ S 65°17′08″ W), 1190 m (MLP 6545-1); small spring near Tiraxi (23°59′57″ S, 65°19′39″ W), 1576 m (MLP 6553); on the road between Termas de Reyes and Laguna Yala, flooded areas at the bottom of hills (24°07′47″ S, 65°28′58″ W), 1920 m (MLP 7371). Salta Province: unnamed brook at national road No. 40 at Molinos (25°18′53″ S, 66°14′58″ W), 2155 m (MLP 6526); small spring at road No. 33 to Cachi at Los Laureles (25°06′27″ S, 65°36′10″ W), 1360 m (MLP 6529); Tucumán Province: flooded areas at side of the Nío River, near Río del Nío City (26°25.60′ S 64°55.60′ W), 886 m (MLP 7403); on side of Medina River, on provincial road No. 305, between El Tipal and Aserradero (MLP 7404-1); small pond on side of Potrero de Las Tablas River, Raco, 880 m (MLP6992), La Angostura dam, on Los Sosa River (26°55′21″ S, 65°41′02″ W), 2000 m (MLP 6897-2).



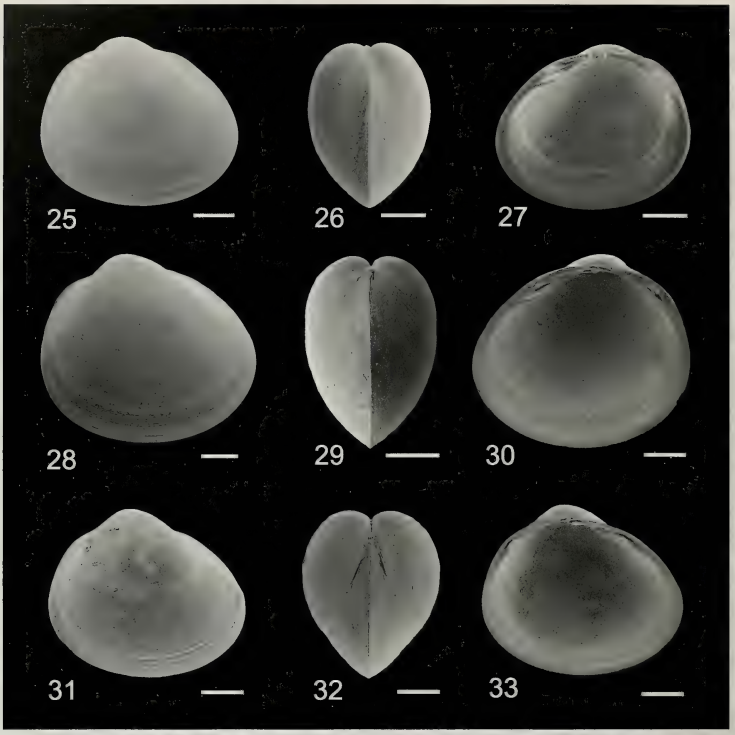
Figures 23–24. *Pisidium ocloya* new species. **23.** Gross anatomy. **24.** Detail of nephridium. (**id:** inner demibranch; **irm:** inner radial mantle muscles; **n:** nephridium; **p:** pericardium; **pa:** posterior adductor; **r:** rectum.

Distribution: Catamarca, Jujuy, Salta, and Tucumán provinces, Argentina, between 880 and 2155 m altitude.

Etymology: The name of the new species refers to the Ocloyas, ancient aboriginal inhabitants of the lands in the surroundings of the type locality.

Remarks: *Pisidium ocloya* new species strikingly differs from other northwestern Argentine *Pisidium* species by its relatively small size and trapezoidal shell outline. Compared with *Pisidium vile* Pilsbry, 1987, a small species from the eastern drainage system of the Río de La Plata Basin, *P. ocloya* new species differs in being larger and comparatively lower. Ituarte (1999) described *Pisidium huillichum* from southern Chile, another small-sized *Pisidium* species with one mantle opening and one demibranch, which differs from *P. ocloya* in having a non trapezoidal shell outline, lower beaks, very strong lateral teeth, and strongly marked commarginal ribs of the shell surface.

The height/length ratio, the convexity index and the degree at which part of the ligament is protruded showed a relatively wide variability in samples of *Pisidium ocloya* from different localities (Figures 25–33); larger specimens were in general more convex with much inflated and pronounced beaks, and more sharply defined trapezoidal outline.



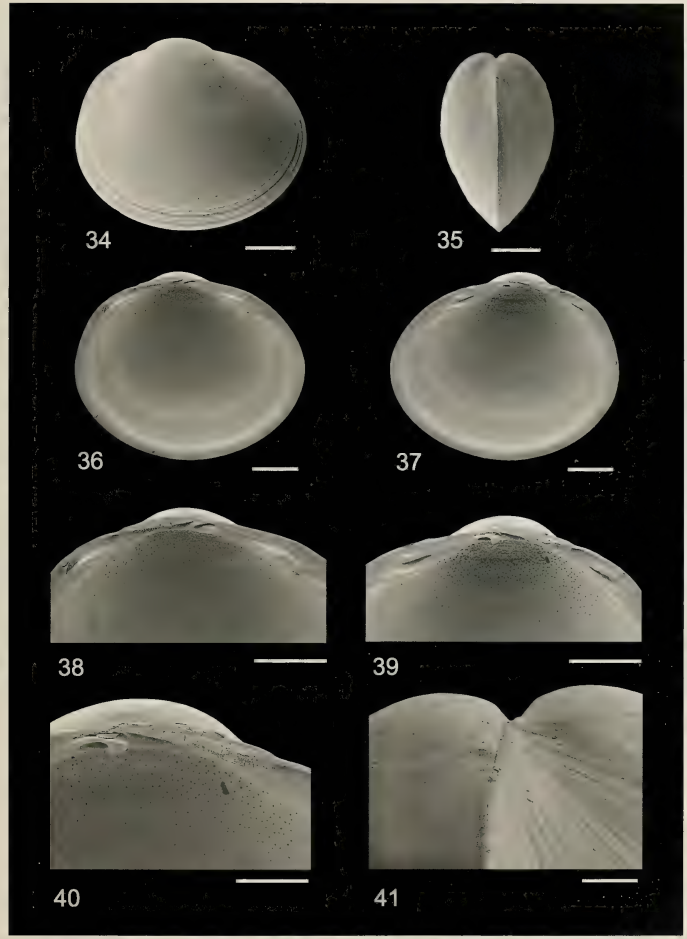
Figures 25–33. *Pisidium ocloya* new species. **25–27.** Specimens from Termas de Reyes, Jujuy (MLP 5497-1). **28–30.** Specimens from Zapla, Jujuy (MLP 6899-2). **31–33.** Specimens from Cachi, Salta (MLP 6529). Scale bars = 500 µm.

Pisidium chicha new species
(Figures 34–43)

Diagnosis: Rather elliptic shell outline, sub-centrally located beaks, somewhat inflated and markedly raised from shell surface, are diagnostic features. The presence of only one mantle aperture and one demibranch is also distinctive.

Description: Shell small, maximum observed shell length 2.7, moderately high (mean HI = 79 ± 1), not convex (mean Ci = 68 ± 5); shell outline strikingly oval. Dorsal and ventral margins broad, dorsal margin, slightly arcuate, ventral margin uniformly curved; anterior end evenly curve and only slightly projected forward, posterior end slightly truncated (Figures 34–37). Beaks wide, widely rounded at tip, somewhat inflated, raised above dorsal margin but low, sub-central, slightly displaced backward, located at about 57–58% of SL. Shell surface glossy, amber, sculptured with well marked fine and rather regularly spaced striae (Figure 34).

Hinge plate narrow, hinge line somewhat short, HiL/SL = 53 ± 3% of SL (n = 8), widely curved. Hinge on left valve (Figures 36, 38): cardinal teeth well-developed, the inner one (C_2) thin, long, straight at base, bent upward distally, parallel with respect to antero-posterior axis, rounded at tip, outer one (C_4) a slender, slightly



Figures 34–41. *Pisidium chicha* new species. **34.** Holotype (MLP 6899-1-1): outer view of right valve. **35–41.** Paratypes (MLP 6899-1-2). **35.** Posterior view. **36.** Left valve, inner view. **37.** Right valve, inner view. **38.** Left valve, detail of hinge. **39.** Right valve, detail of hinge. **40.** Right valve, detail of cardinal tooth and ligament. **41.** Posterior view, detail of ligament. Scale bars (**34–37**) = 500 μm; (**38, 39**) = 200 μm; (**40**) = 250 μm; (**41**) = 100 μm.

curved blade, quite oblique, overlapping C_2 on posterior half; anterior lateral tooth (AII) very strong, straight, cusp high, somewhat acute, displaced distally; posterior lateral tooth (PII) short, strong, cusp high, distal. Hinge on right valve (Figures 37, 39, 40): cardinal tooth (C_3) well-developed, narrow, and evenly curved on anterior half, quite enlarged into triangular, slightly grooved cup at posterior end; slightly hanging from inner margin of hinge plate. Lateral teeth short and robust, inner anterior lateral (AI) somewhat curved, cusp displaced forward; outer anterior lateral tooth (AIII) very short, straight, with distal cusp; inner posterior lateral one (PI) short, straight, slender and low, cusp sub-central; outer posterior lateral one (PIII) minute, with distal cusp.

Escutcheon lanceolate, long, outline demarcated by a very delicate line. Ligament-pit enclosed, inner margin gently sinuous (Figures 40, 41). Ligament moderately strong, internal, slightly visible from exterior, but not protruded, representing about 23% of shell length.

Anatomy: Only one (anal) mantle opening present. Only inner demibranch present (Figure 42). Inner radial mantle muscles weak, inserted just above or coalescent with pallial line. Nephridium with dorsally visible lateral loop (Figure 43).

Type Locality: Unnamed brook flooding into Zapla River in the neighborhood of Zapla City (24°16′01″ S, 65°07′09″ W), 946 m altitude, Jujuy Province, Argentina, and small springs on bank of Manzanito Rivulet, on the road from Santa Victoria East to Yavi near Huertas (22°14′20″ S, 35°00′31″ W), 2740 m, Jujuy Province, Argentina.

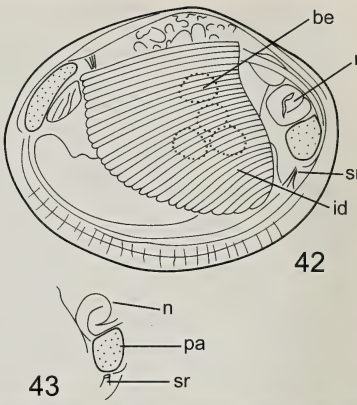
Type Material: Holotype (MLP6899-1-1), 9 paratypes (7 paratypes MLP 6899-1-2; 2 paratypes MACN-In 36363) from 24°16′ S, 65°12′ W; 62 paratypes from 22°14′20″ S, 35°00′31″ W (52 paratypes MLP 6550; 5 paratypes FML 14775; 5 paratypes MNHN).

Other Material Examined: Catamarca Province: flooded areas at side of an unnamed river on the road to Singuil, (27°38′25″ S, 65°57′23″ W), 2000 m (MLP7203). Jujuy Province: Los Cedros Rivulet, close to Las Maderas Dam (24°28′40″ S 65°17′08″ W), 1190 m (MLP 6545-2). Tucumán Province: small pools at the side of Medina River, on provincial road 305 between El Tipal and Aserradero (MLP 7404-2).

Distribution: Catamarca, Jujuy and Tucumán provinces, Argentina, between 940 and 2740 m altitude.

Etymology: The name of the new species alludes to the Chichas, a small ethnic group that was a part of the Omaguaca people, who inhabited the lands in the neighborhood of the type locality.

Remarks: The shell shape, quite ovate and nearly equilateral, and the marked sculpture of *Pisidium chicha* new species are distinctive features that allow for easy identification of the new species among other *Pisidium* species from northwestern Argentina. A moderate shell



Figures 42–43. *Pisidium chicha* new species. **42.** Gross anatomy. **43.** Detail of nephridium. (**be:** brooding embryos; **id:** inner demibranch; **n:** nephridium; **pa:** posterior adductor; **sr:** siphon retractor).

variation was observed: the specimens from Manzanito Rivulet (MLP 6550) show shells slightly more convex and higher than those of the specimens from Zapla (MLP 6899-1); the striae were slightly coarser and more marked in the former group. Specimens from Catamarca Province (MLP 7203) show slightly inequilateral shells, with posterior end slightly shorter. *Pisidium chicha* shares with *P. ocloya* the same number of mantle openings and demibranchs and the nephridium with lateral lobe dorsally visible; but the former species strikingly differs in having a smaller shell with quite an oval shell outline. The presences of only one demibranch and one mantle opening in *P. chicha* clearly separate this species from *P. chiquitanum*. In addition, this latter is a larger species of relatively similar shell outline but that also differs from *P. chicha* in having an almost smooth shell surface, lower, more backward displaced beaks, and somewhat truncated posterior end.

Pisidium chiquitanum Ituarte, 2001
(Figures 44–47)

Pisidium chiquitanum Ituarte, 2001: 50; figs. 2–14 (La Siberia, West of Comarapa, Santa Cruz de La Sierra, Bolivia, holotype MHNB 34734).

Diagnosis: Rather elongate shell outline, slightly truncated at posterior end, low and posteriorly located beaks, ligament position, internal but externally visible, presence of branchial and anal openings, two demibranchs on each side and nephridia of closed type.

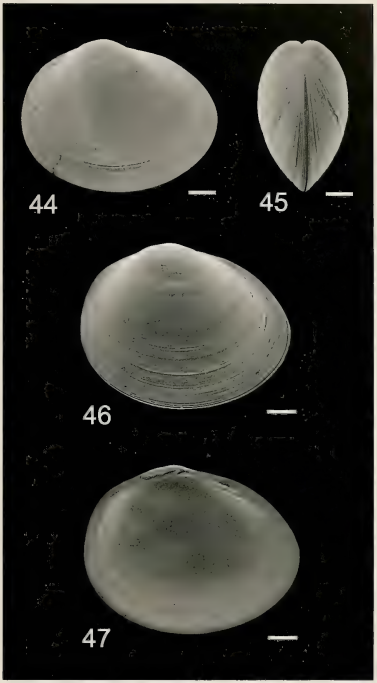
Description: Shell thin, small to medium size (mean SL = 3.9 ± 0.25; maximum observed size: 4.2 mm), not very high (mean HI = 80 ± 1), not convex (mean Ci = 61 ± 4), shell outline markedly oval, elongate, anteriorly produced, posterior end short, widely rounded, or slightly truncated and nearly straight (Figures 44, 46, 47). Beaks low, depressed, slightly projected above dorsal margin, located at about 62% of SL (Figures 44–46). Shell surface dull glossy, straw-yellowish, with fine and low commarginal striae, moderately more accentuated towards the shell margin (Figures 44, 46).

Hinge plate solid, hinge line rather long (HiL/SL = 56 ± 2). Hinge on right valve: Right cardinal tooth (C_3) strongly curved in middle, quite narrow on anterior half, enlarged into gently sulcated, rounded, or somewhat elongate cup. Right lateral teeth robust, inner anterior lateral (AI), widely curved, long, cusp sub-central or slightly displaced forward; outer anterior lateral tooth (AIII) quite short, cusp distal; inner posterior lateral (PI) nearly straight, short, cusp sub-central; outer posterior lateral tooth (PIII) reduced in size with distal cusp. Left valve (Figure 47): cardinal teeth short, inner one (C_2) short, oblique with respect to antero-posterior axis, outer one (C_4) a narrow curved lame, quite oblique, overlapping C_2 on posterior half; anterior lateral tooth (AII) strong, straight, cusp sub-central; posterior lateral tooth (PII) narrow and weak, cusp distal.

Ligament-pit enclosed, deep, inner margin slightly sinuous, concave at posterior end. Escutcheon well marked by a delicate line; ligament long, internal, but visible from outside in anterior half through a very narrow and sometimes rather long gap between valves, never protruded. Ligament length is 23 ± 1% of shell length.

Anatomy: Anal siphon and branchial mantle opening present. Presiphonal suture rather long, representing 11 ± 2% of SL. Anal siphon well-developed, pair of powerful siphonal retractors present. Inner radial mantle muscles, 8 bundles as rule, inserted away from pallial line, scars of those corresponding to anal siphon retractors coalescent with posterior adductor muscle scars. Inner and outer demibranchs present. Outer demibranch reduced in size, composed of 11–15 very short descending filaments, reaching back to the 14–16th filament of inner demibranch. Nephridia of closed type, dorsal lobe variable in shape, commonly subquadrate, with lateral loop not visible in dorsal view.

Material Examined: Holotype (MHNB 34734) La Siberia, West of Comarapa, Santa Cruz de La Sierra, Bolivia; Tucumán, Argentina: 27°01′24″ S, 65°39′29″ W (MLP 6554); Cerro Muñoz, Santa Cruz, 26°54′ S, 65°46′42″ W, 2400 m (MLP 6991); La Angostura dam, 26°56′ S, 65°41′03″ W, 1800 m (MLP 6527); Jujuy, Argentina: Los Laureles, 25°06′27″ S, 65°36′10″ W, 1360 m (MLP 6528); Los Toldos, Santa Victoria Department, 1770 m (MLP 6993); small brook near Tiraxi (23°59′57″ S, 65°19′39″ W), 1576 m (MLP 6552); small spring at the side of provincial road No. 4, near Termas de Reyes (24°10′36″ S, 65°28′18″ W) (MLP 5497-2).



Figures 44–47. *Pisidium chiquitanum* Ituarte, 2001. **44, 45.** Paratype (MLP 5362). **44.** Outer view of right valve. **45.** Posterior view. **46, 47.** Specimen from Tiraxi, Jujuy (MLP 6552). **46.** Outer view of right valve. **47.** Inner view of left valve. Scale bars = 500 μm.

Distribution: Ranging from sub-Andean regions in Siberia (west of Comarapa) in central Bolivia (1800 m altitude) southward to northwestern Argentina (between 1360 and 2400 m altitude).

Remarks: *Pisidium chiquitanum* can be easily identified among South American *Pisidium* species by its oval shell outline with low beaks and internal (however visible from the outside) ligament. It is also characterized by two, inner and outer, demibranchs on each side, two siphonal openings, and nephridia of closed type.

Pisidium chiquitanum resembles *Pisidium meierbrooki* Kuiper and Hinz, 1984, from Peru and Bolivia, which is the only known species from tropical South America with both, branchial and anal, siphonal openings (Ituarte, 1995). *Pisidium meierbrooki* differs from *P. chiquitanum* in having a more convex shell (according to data in Kuiper and Hinz, 1984, the Ci varies between 77 and 80), fuller and more backward displaced beaks. As pointed out by Ituarte (2001)*Pisidium chiquitanum* is similar to specimens from Ecuador and Peru reported by Kuiper and Hinz (1984), as *Pisidium casertanum* (Poli, 1791), an Eurasian species extremely variable in shell shape, currently reported as cosmopolitan (Burch, 1975; Kuiper, 1983; Kuiper and Hinz, 1984; Holopainen and Kuiper, 1982). However, these specimens are larger than *P. chiquitanum*, having more central beaks and less produced anterior end. *P. chiquitanum* also differs from *P. casertanum* in having less convex shell, lower and narrower beaks, decidedly displaced backward. The specimens from northwestern Argentina slightly differ from the ones from Bolivia in being generally higher, with beaks slightly less displaced in posterior direction (Figure 46).

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Mysella pedroana, a commensal bivalve (Lasaeidae) on two decapod crustacean hosts

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ABSTRACT

Mysella pedroana (Dall, 1898), lives commensally on *Isocheles pilosus* (Holmes, 1900), and *Blepharipoda occidentalis* Randall, 1839. Because of their small size at reproductive maturity, specimens attached to *Isocheles pilosus* were previously referred to in the literature as an undescribed species. However, preliminary comparisons between the variability of hinge dentition and internal structure of those specimens and small individuals of *Mysella pedroana* indicate that they represent instead a single species. Variability of characters including size at reproductive maturity and shell morphology suggests that *Mysella pedroana* is a highly variable species.

INTRODUCTION

A small bivalve living attached to hermit crabs has perplexed biologists for over a decade. It was referred to as *Mysella* sp. H by Valentich-Scott and Barwick (2001), as an undescribed species. It was shown to be reproductively mature at 1.0 mm in length.

Bivalves in the family Lasaeidae have been taxonomically problematic (Dall, 1898; Gage, 1966a; 1966b; Ó Foighil and Eernisse 1988; Morton and Scott, 1989). These bivalves combine features of immaturity induced by changes in environmental factors, perhaps due to their commensal nature. *Mysella pedroana* (Dall, 1898), is no exception. It is found both as a commensal and free-living (Scott, 1987); however, due to its prevalence on hosts, it may prefer a commensal habitat.

Mysella pedroana was previously thought to be host-specific and found only on the sand crab *Blepharipoda occidentalis* Randall, 1839, (Burch and Burch, 1944; Boss, 1965a; Lafferty, 1993; Boyko and Mikkelsen, 2002). Originally described by Dall in 1898 from a single valve, *M. pedroana* was then redescribed (Boyko and Mikkelsen, 2002) and associated with *B. occidentalis* as host. The discovery of its occurrence on another host, the hermit crab *Isocheles pilosus* (Holmes, 1900), previously undocumented variation in shell morphology, and small size at reproductive maturity has led to this present study.

Blepharipoda occidentalis (Decapoda: Albuneidae) is found in the northeastern Pacific from Stinson Beach, Marin County, California, USA, to Bahia Santa Rosalia, Baja California, Mexico (Morris et al., 1980) both intertidally and subtidally, burrowing in sand. *Isocheles pilosus* (Decapoda: Diogenidae) ranges from Bodega Bay Harbor, Sonoma County, California, USA, to Estero de Punta Banda, Baja California, Mexico (Rickets et al., 1985). Like *B. occidentalis*, it is intertidal, but also occurs in mud flats, bays and estuaries including depths offshore up to 55 meters. *Isocheles pilosus* most commonly inhabits shells of *Polinices* or *Kelletia* (pers. comm. Scott, 2004) and crawls on the sand or buries with only its eyes and mouth visible (Fager, 1968). *Mysella pedroana* is either attached to the crab's setae or in its branchial chambers.

MATERIALS AND METHODS

Preserved specimens identified by Valentich-Scott and Barwick (2001) as *Mysella* sp. H from the collections in the Santa Barbara Museum of Natural History (SBMNH) were studied. Additional material included SBMNH specimens associated with preserved specimens of *Isocheles pilosus* and *B. occidentalis*, along with specimens from two living *I. pilosus* and one *B. occidentalis* collected at Sands Beach, Santa Barbara. Specimens removed from *I. pilosus* are deposited as SBMNH 351472–351480 and 47635. Material of *M. pedroana* examined includes SBMNH 348251, 345553, 348252, and 348253.

Of the 145 available specimens, 35 were opened and examined for gross anatomy. Characters examined were internal structure, shell dentition, and shape. Measurements were made with vernier calipers and anatomical observations were performed under a dissecting microscope. Scanning electron micrography was performed at SBMNH with a Zeiss EVO 40 XVP with a variable-pressure secondary electron detector.

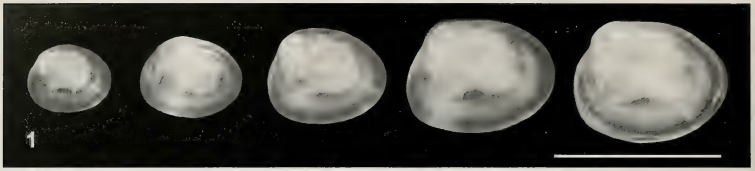


Figure 1. A growth series of commensal *Mysella pedroana*, SBMNH 351473. Scale bar = 1 mm.

Living *Mysella perdroana* were placed in Petri dishes with sea water and coarse sediment for comparison of movement in different media. Specimen with brood was stained with crystal violet in distilled water prior to examination.

RESULTS

Mysella pedroana (Dall, 1898)

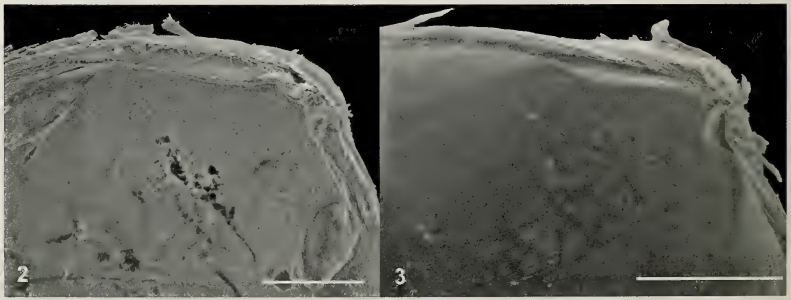
Description: Shell (Figures 1–3): Shell morphology variable from ovate to subtrigonal, thin, more elongate anteriorly; umbones opisthogyrate; beaks range from central to posterior; shell surface white with poorly defined commarginal striae; periostracum thick and yellow, variable in texture, rough and dehiscent to smooth and adherent; prodissoconch line present; maximum shell length 11.0 mm, mean height to length ratio 77% (herein) (SD ±4.8; range 11.0–1.0 mm) to 80% (Boyko and Mikkelsen, 2002).

Muscle scars apparent in larger specimens with anterior adductor scar elongate and posterior ovate; pallial line entire; hinge with prominent subumbonal resilium; two lateral cardinal teeth on right valve with longer anterior tooth and slight groove, posterior shorter; teeth diverging into an inverted V; left valve with thin grooves (lamellae) that interlock with the right valve. Extensive variation shown in smaller specimens (length 1–3.4 mm), which may exhibit a posterior tubercular tooth on the right valve with a similar posterior tubercular tooth on the left valve.

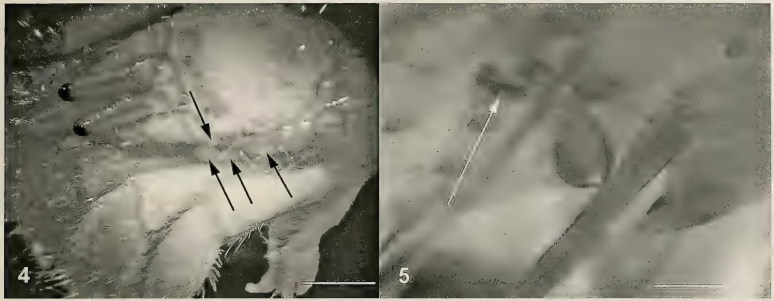
Gross Anatomy: Mantle papillate, more so anteriorly; ctenidium encompasses large area of internal space and serves as a brood chamber; presence of eggs observed in specimens from 1–11 mm in length; labial palps small.

Observations on Live Specimens: Activity was enhanced following regular replacing of cold sea water. Clams were observed crawling on surface of Petri dish with shell positioned vertically, in the manner of a gastropod; dug in sand with anterior end, process took 15–20 sec. Detached *M. pedroana* took 3 min. to reattach to setae on the ventral surface of *I. pilosus*. However, when *I. pilosus* setae were easily accessible and *M. pedroana* was placed next to them, attachment took 30–45 sec.

Host information and prevalence: *Blepharipoda occidentalis* had a carapace length of 4.06–4.55 cm (n = 3) and all three had *Mysella pedroana* present. *Isocheles pilosus* had a carapace length of 1.9–2.57 cm (n = 6) with three of the six crabs having bivalves present.



Figures 2–3. *Mysella pedroana*, hinge dentition. **2.** From host *Isocheles pilosus*, SBMNH 351473, SEM. Scale bar = 200 µm. **3.** From host *Blepharipoda occidentalis*, SBMNH 351478, SEM. Scale bar = 1 mm.



Figures 4–5. *Mysella pedroana*. **4.** Host *Isocheles pilosus* showing attachment between the chela and carapace (arrows), SBMNH 345553, Scale bar = 2.2 mm. **5.** On host *Isocheles pilosus* with byssus (arrow), SBMNH 351472. Scale bar = 0.8 mm.

Three *B. occidentalis* were examined with 100% prevalence. Of the six preserved museum specimens of *I. pilosus*, only one was infested. However, two live *I. pilosus* were examined and fifty-nine *M. pedroana* specimens were retrieved.

The live *B. occidentalis* examined had two *M. pedroana* that were found on the external surface near the antennae and on the second pereopod.

Host *Isocheles pilosus*: *Mysella* specimens on *I. pilosus* were found in the branchial chambers, attached to the chelae, the junction between the chela and carapace, the ventral setae and branchial chambers (Figure 4). The largest specimens were on the chelae (1 mm) with smaller individuals on the ventral surface (0.7–1 mm) and juveniles (<0.7 mm) anteriorly in the right and left branchial chambers. Those on the ventral surface and in the branchial chambers were attached with byssus (Figure 5). The few on the chelae were observed crawling or attached by byssal threads to the surface spines of the chelae. Upon preservation in 70% ETOH *M. pedroana* retained its byssal threads.

DISCUSSION

This study suggests that shell shape of *Mysella pedroana* is more variable than previously appreciated. These variable characteristics include texture of the periostracum (rough and dehiscent to smooth and adherent), dentition, shape of the shell. These differences have been attributed to environmental conditions in other molluscan shells (Wellington and Kuris, 1983; De Wolf et al., 1998).

Shell variation probably led to the redescription of *Mysella pedroana* as *Rochefortia golischi* by Dall in 1916 (Burch and Burch, 1944); these were later synonymized by Scott (1987). However, this variation is also common to many commensal species and makes it difficult to identify them based on shell morphology (Ó Foighil and Eernisse, 1988; Morton and Scott, 1989).

Due to shell variation and the small size at reproductive maturity of *M. pedroana*, these smaller bivalves on *I. pilosus* were thought to be a new species, referred to as *Mysella* sp. H (Valentich-Scott and Barwick, 2001). However, minimum size of brooding adults of *M. pedroana* had been previously reported at 1 mm (Valentich-Scott and Barwick, 2001) and spermatogenesis has been confirmed in specimens of 1.2 mm. Previous observations for individuals of *M. pedroana* undergoing spermatogenesis were 4.7 mm in length (pers. comm. Kevin Lafferty, 2004). Reproductive maturity at small sizes has been reported also for *Pseudopythina macrophthalmensis* at 2.0 mm (Jespersen et al., 2001) and *Mysella bidentata* with egg production at 1.7 mm (Ó Foighil et al., 1984).

The prevalence of *Mysella pedroana* was higher on *B. occidentalis* than on *I. pilosus*. Those on *B. occidentalis* were also larger in the gill chambers compared to only juveniles found in the gills of *I. pilosus*. Further examination of both hosts would be required to see if there is a host preference.

Reattachment to a host is possible for the species. Both Lafferty (pers. comm. 2004) and Valentich-Scott (pers. comm. 2004) noted that individuals could drop their byssus and disassociate from the host if perturbed. Individuals of *M. pedroana* could use this procedure to move from host to host or to become free-living.

The above observations on morphology and symbiont-host relationships permit the identification of this bivalve as *Mysella pedroana*. Previously reported host specificity for commensal bivalves may be due to the scarcity of studies or experimental observations (Boss, 1965b; Morton and Scott, 1989). This species was previously thought to be host-specific (Boyko and Mikkelsen, 2002), an assumption here shown not to be valid.

ACKNOWLEDGMENTS

I would like to thank to Paul Valentich-Scott for his guidance, knowledge and for introducing me to the world of bivalves. The Hearst Foundation Internship through the Santa Barbara Museum of Natural History made this research possible. Scanning electron microscope facilities funded by NSF grant number MRI0420726, Daniel Geiger assisted with SEM images. Michael Caterino, Henry Chaney and Armand Kuris for reviewing preliminary drafts. Shane Anderson provided living crabs, Patricia Sadeghian contributed her knowledge of crustaceans. Paula Mikkelsen and Kevin Lafferty whom offered additional data. Kelvin Barwick contributed many specimens. Two anonymous reviewers offered critical observations which greatly improved the manuscript.

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Coralliophila trigoi (Gastropoda: Muricidae), a new species from the northeastern Atlantic Ocean

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ABSTRACT

Based on shell characters and with further support from molecular data, *Coralliophila trigoi*, a new species of gastropod of the family Muricidea, is here described from the northeastern Atlantic Ocean. The new taxon, consisting of several specimens mainly collected along the Atlantic Spanish coast, has previously been misidentified in the literature as *Coralliophila basilea* (Dautzenberg and H. Fisher, 1896). *Coralliophila trigoi* new species is conchologically similar to *Coralliophila meyendorffii* (Calcara, 1845), and *Coralliophila panormitana* (Monterosato, 1869), but it can be easily separated from them mainly because it is differently sculptured. The new species is compared with other members of the genus *Coralliophila* from the same geographical area and Mediterranean Sea. Molecular sequencing of the internal transcribed spacer 2 region (ITS2) of the nuclear rDNA and part of the mitochondrial gene for 12S rDNA confirm the validity of the new species.

INTRODUCTION

The coralliophilines form a monophyletic group of neogastropods that includes approximately 200–250 described species grouped, based on their shell morphology, in at least 7–10 "genera", distributed worldwide in temperate and tropical oceans. The subfamily Coralliophilinae Chenu, 1859 (for the phylogenetic relationship of this muricoidean groups, see Oliverio and Mariottini, 2001a) includes species invariably associated with cnidarians, which are generally used as food by the gastropods. Shell variability, absence of radula, absence of a preserved protoconch (often eroded in adults and even in young specimens), together with a limited knowledge of the anatomy, represent constrains to the understanding of the taxonomic status of this group of neogastropods. Their classical systematics above the species level is at present far from being stable (Clover, 1982; Bouchet and Warén, 1985; Kosuge and Suzuki, 1985; Oliverio, 1989; Vaught; 1989; Oliverio, in press). Data from mitochondrial and nuclear genes (12S rDNA and ITS2 rDNA, respectively) have been recently utilized in the proposal of a molecular framework for the phylogeny of these muricids (Oliverio and Mariottini, 2001a; Oliverio, Cervelli and Mariottini, 2002). Data from both sequence and secondary structure show that Rapaninae Gray, 1853 (=Thaidinae Jousseaume, 1888) are their sister group (Harasewych et al., 1997; Oliverio and Mariottini, 2001a; Oliverio, Cervelli and Mariottini, 2002), indicating a monophyletic radiation of the Coralliophilinae. The state-of-the-art knowledge about feeding, anatomy, sexual strategies, parental care, and protoconch of coralliophilines was recently reviewed by Richter and Luque (2002). The authors reported the available data on protoconch and larval development of many coralliophilines belonging to ten different genera, including *Coralliophila* H. and A. Adams, 1853. We had the opportunity to examine several shells of a coralliophiline that we could allocate to any of the Atlantic and Mediterranean species of this subfamily. These shells, mostly collected along the coast of Galicia, Spain, were previously misidentified in the literature as *Coralliophila basilea* (Dautzenberg and H. Fisher, 1896) (Rolán, 1983; Rolán, López and Gutiérrez-García, 1995). After comparisons with other species, we realized that they represent an undescribed species, possibly related to *Coralliophila meyendorffii* (Calcara, 1845) and *Coralliophila panormitana* (Monterosato, 1869).

In order to verify the taxonomic validity of *Coralliophila trigoi*, we carried out molecular sequencing of the internal transcribed spacer 2 region (ITS2) of the nuclear rDNA and of part of the mitochondrial gene for 12S rDNA. Genomic DNA was extracted from the dissected foot of two freshly collected individuals with standard methods (SDS-proteinase K digestion, phenol/chloroform extraction, ethanol precipitation (Oliverio and Mariottini, 2001b)). Mitochondrial rDNA was amplified through the polymerase chain reaction (PCR) with primers *12S-I* and *12S-III* (Oliverio and Mariottini, 2001a). Nuclear ribosomal ITS2 was amplified using the primers

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Table 1. Collecting data and DDBJ/EMBL/GenBank accession number for specimens assayed in molecular systematics.

Species/individuals	Collecting locality and depth	Accession number	
		12S	ITS2
Coralliophila neritoidea	Taiwan, 23°10′ N, 120°05′ E, 5 m depth	AJ293679	AJ420258
Coralliophila brevis	La Maddalena Is. (Sardinia, Italy), 41°15′ N, 009°26′ E, 30 m depth	AJ293676	AJ420256
Coralliophila mejendorffii	La Maddalena Is. (Sardinia, Italy), 41°15′ N, 009°26′ E, 3–7 m depth	AJ297517	AJ293661
Coralliophila panormitana	Cape Circeo (Latium, Italy), 41°11′ N, 013°04′ E, 70 m depth	AJ293681	AJ420259
Coralliophila trigoi new species, specim. #1	Camariñas, Galicia, Spain, northeastern Atlantic Ocean, 15–50 m depth	AJ937305	AJ937307
Coralliophila trigoi new species, specim. #2	Camariñas, Galicia, Spain, northeastern Atlantic Ocean, 15–50 m depth	AJ937306	AJ937308

its-3d and *its-4r* complementary to conserved regions of the ribosomal coding portions on the 5.8S and 28S rRNAs (Oliverio and Mariottini, 2001b). PCR-amplified products were directly sequenced by an automated sequencer. Nucleotide sequences were first aligned by hand and the alignment progressively optimized according to secondary structure homology. Phylogenetic analyses were performed using PAUP* 4b10 (Swofford, 2002). GenBank accession numbers (12S and ITS2) of the *Coralliophila trigoi* sequences are reported in Table 1.

Institutional abbreviations used: MNCM, Museo Nacional de Ciencias Naturales, Madrid, Spain; MZB, Laboratorio di Malacologia, Museo di Zoologia dell'Università di Bologna, Italy.

Abbreviations used for collections: CS-PM, Carlo Smriglio and Paolo Mariottini (Rome, Italy); ER, Emilio Rolán (Vigo, Spain); FS, Frank Swinnen (Lommel, Belgium); JT, Juan Trigo (Brion, A Coruna, Spain); MO, Marco Oliverio (Rome, Italy).

SYSTEMATICS

Superfamily Muricoidea Rafinesque, 1815
Family Muricidae Rafinesque, 1815
Subfamily Coralliophilinae Chenu, 1859
Genus *Coralliophila* H. and A. Adams, 1853

Type Species: *Fusus neritoideus* Lamarck, 1816, Ency. Meth., pl. 435, figs. 2a–b. (=*Purpura violacea* Kiener, 1836), by subsequent designation (Iredale, 1912). Recent, Indo-Pacific.

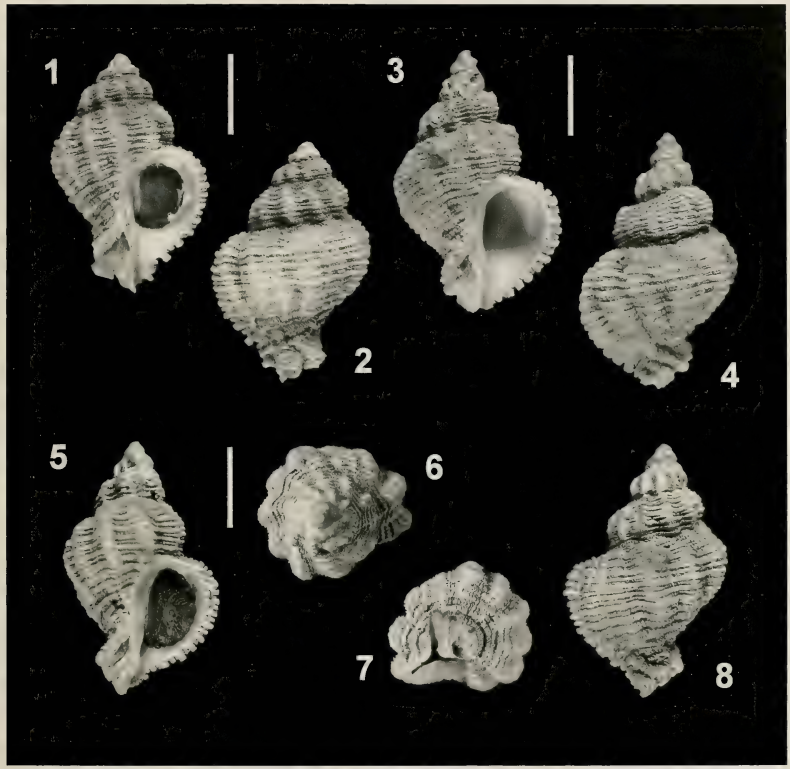
Coralliophila trigoi new species
(Figures 1–8, 13–14, 17–21)

Description: Shell of large size, up to 35 mm length. Protoconch usually eroded in adult specimens (protoconch observed in only one juvenile specimen, albeit worn and lacking the embryonic stage). Protoconch indicative of planktotrophic larval development, multispiral, composed of protoconch I and II. Protoconch II of about 2½ whorls, with a diameter of about 800 μm, showing two strong spiral keels, only one visible above the suture of the first whorl, crossed by axial ribs forming nodules at intersections. The protoconch-teleoconch demarcation is well-defined, marked by a varix. Teleoconch shape biconical, elongate ovoid-fusiform, solid, rather inflated. Spire relatively high, conical, 4–5 rather convex whorls, shoulder rounded. Suture not very evident, partially covered by the sculpture, which is formed of 15–20 spiral cords, regularly ordered, rarely alternating with smaller spiral cords. Spiral sculpture consisting of ribs rounded in cross-section, all of similar width, densely covered with imbricating, fine, and long lamellae. Axial ribs 7–11, large, generally weak, crossing the spiral cords. Siphonal canal short, narrow, open, moderately curved. Aperture large, oval, representing about half of the shell height, white or cream-white inside. Umbilicus absent. Outer lip thin and crenulate. Shell color uniformly reddish- or pale-brown. Operculum oval, oblong, horny, concentric, with lateral-terminal nucleus, reddish-brown.

Type Material (Figures 1–8): Holotype (Figures 1–2), 30.6 × 20.4 mm, MNCN 15.05/46458; paratype A (Figures 3–4), 31.6 × 19.4 mm, MZB 31023; paratype B (Figures 5–8), 27.3 × 16.7 mm, CS-PM; paratype C, 27.4 × 18.2 mm, CS-PM; paratype D, 24.2 × 16.8 mm, ER; paratype E, 26.8 × 16.6 mm, ER; paratypes A–E, from type locality; paratype F, 30.9 × 18.5 mm, ER, Malpica, Spain; paratype G, 23.5 × 16.3 mm, ER, Camelle, Spain; paratype H, 24.8 × 17.3 mm, JT; paratype I, 21.2 × 12.3 mm, JT; paratype L, 26.9 × 17.1 mm, JT; paratype M, 21.4 × 12.3 mm, JT; paratype N, 31.2 × 18.0 mm, JT; paratype O, 18.5 × 12.8 mm, JT; paratype P, 7.4 × 5.1 mm, CS-PM; paratypes H–P from Porto da Baleeira, Sagres, Portugal; paratype Q, 30.2 × 18.1 mm, ER, Lira A Coruña, Spain; paratype R, 26.4 × 17.2 mm, ER, Malpica, Spain; paratype S, 27.3 × 16.2 mm, CS-PM; paratype T, 25.1 × 16.2 mm, CS-PM; paratypes Q–T from Lira A Coruña, Spain; paratype U, 39.2 × 23.2 mm, CS-PM, A Guarda, Spain; paratype V, 30.1 × 18.6 mm, CS-PM, type locality; paratype W, 29.8 × 17.4 mm, CS-PM; paratype Z, 25.8 × 16.2 mm, CS-PM; paratypes W–Z from Malpica, Spain.

Type Locality: Camariñas, Galicia, Spain, northeastern Atlantic Ocean, 15–50 m depth.

Distribution: Known from Galicia, Spain, to Algarve, Portugal, in the Atlantic Ocean, and from Malaga and Almeria (Alboran Sea, Spain) in the Mediterranean.

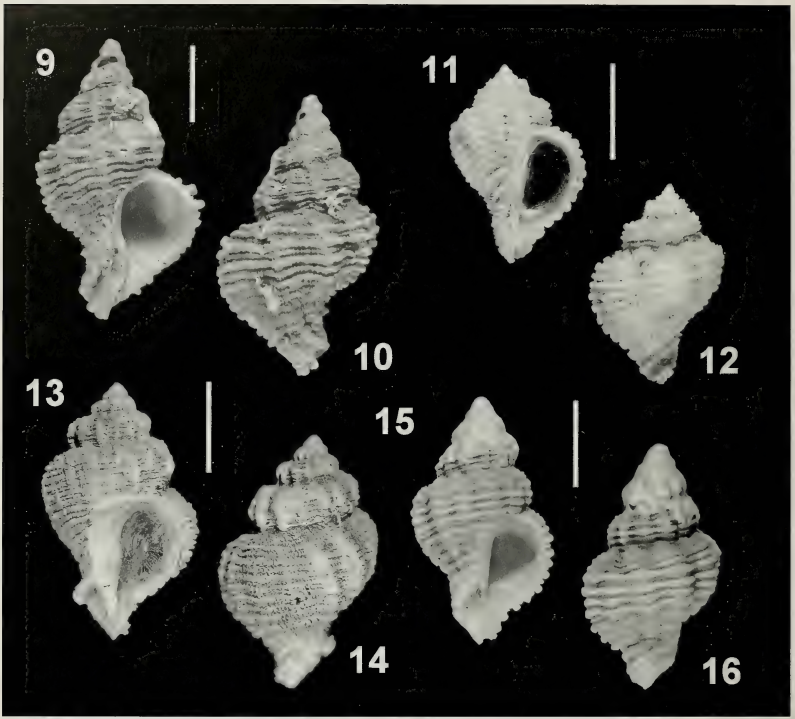


Figures 1–8. *Coralliophila trigoi* new species. **1–2.** Holotype, 30.6 × 20.4 mm, MNCN 15.05/46458. **3–4.** Paratype A, 31.6 × 19.4 mm, MZB 31023. **5–8.** Paratype B, 27.3 × 16.7 mm, CS-PM. From type locality, depth 15–50 m. Scale bars = 1 cm.

Habitat: Several live collected specimens were found attached at the base of host cnidarians *Calliactis parasitica* (Couch) (a sea anemone).

Etymology: This species name is dedicated to our friend Juan Trigo, who supplied some of the specimens of the new species.

Molecular Sequencing: Given the often misleading information conveyed by characters of shell morphology in this group (Oliverio and Mariottini, 2001b), we verified the validity of the new species using a molecular approach. We sequenced the internal transcribed spacer 2 region (ITS2) of the nuclear rDNA and part of the mitochondrial gene for 12S rDNA from individuals of the new taxon and compared them with available sequences of *C. meyendorffii*, *C. panormitana*, and *Coralliophila brevis* (Blainville, 1832), plus *Coralliophila neritoidea* (Lamarck, 1816) as outgroup. Parsimony analysis of the aligned sequences of nuclear and mitochondrial DNA resulted in the tree reported in Figure 27.

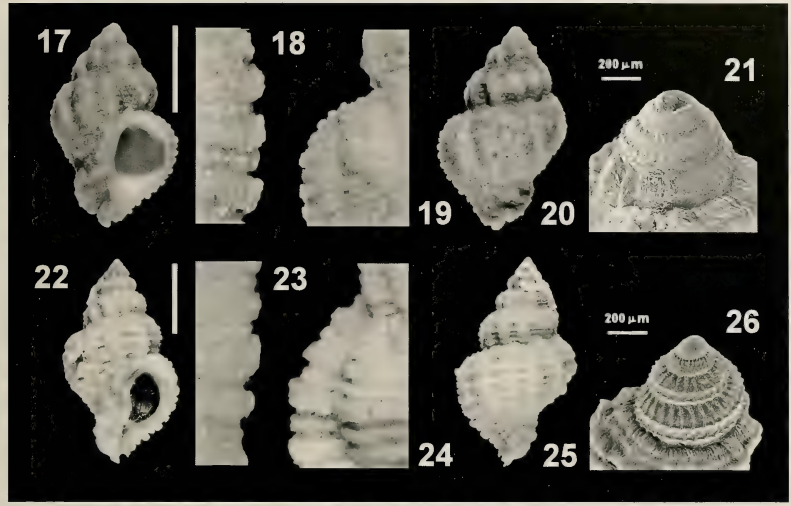


Figures 9–16. Shells of *Coralliophila* species. **9–10.** *Coralliophila squamosa* (Bivona, 1838), 35.9 × 20.9 mm, CS-PM, Camariñas, Galicia, Spain, 15–50 m depth. **11–12.** *Coralliophila panormitana* (Monterosato, 1869), 19.2 × 12.1 mm, CS-PM, Malaga, Spain, 40 m depth. **13–14.** *Coralliophila trigoi* new species, 27.2 × 18.1 mm, MO, Marbella, Spain, 30–50 m depth. **15–16.** *Coralliophila meyendorffii* (Calcara, 1845), 26.8 × 14.7 mm, FS, Punta del Carmen, Lanzarote Isl., Canary Islands, 20 m depth. Scale bars = 1 cm.

The two related species *C. meyendorffii* and *C. panormitana*, were more closely related to each other than to the two specimens of the new species.

Other Material Examined: *Coralliophila trigoi:* 5 spec. from the type locality; 3 spec., Laxe; 1 spec. A Guarda; 3 spec. Camelle; 3 spec. Malpica, Galicia, Spain, ER; 2 spec. Sagres, Algarve, Portugal, CS-PM; 2 spec. Almeria; 3 spec. Marbella, Spain, MO; *Coralliophila meyendorffii:* 10 spec. La Maddalena Isl., Sardinia Island; 1 spec. San Pietro Isl., Sardinia Island; 6 spec. Santa Marinella; 3 spec. Ponza Isl.; 1 spec. Capo Palinuro; 3 spec. Le Castella; 5 spec. Elba Isl., Italy, CS-PM; 6 spec. Punta del Carmen, Lanzarote Isl., Canary Islands, FS; *Coralliophila panormitana:* 5 spec. Marina di Camerota, Italy; 1 spec. Malaga, Spain; 1 spec. Portimão, Portugal, CS-PM; *Coralliophila squamosa:* 23 spec. from the type locality; 6 spec. Laxe; 8 spec. Camelle; 7 spec. Malpica, Galicia, Spain, ER; 10 spec. Ría de Vigo, Galicia, Spain, JT; 1 spec. Malaga, Spain; 1 spec. San Pietro Isl., Sardinia Island; 1 spec. Ventotene Isl.; 1 spec. Marina di Camerata; 2 spec. Le Castella; 2 spec. Civitanova Marche, Italy, CS-PM.

Remarks: Based on shell characters of the teleoconch we take the conservative approach of conserving this



Figures 17–26. Shells of *Coralliophila* species. **17–20.** *Coralliophila trigoi* new species, 23.6 × 14.0 mm, CS-PM, Algarve, Portugal. **18, 19.** Details of shell sculpture. **21.** *Coralliophila trigoi* new species, detail of the larval whorls, paratype P. 7.4 × 5.1 mm, CS-PM, Porto da Baleeira, Sagres, Portugal, 15–25 m depth. **22–25.** *Coralliophila meyendorffii* (Calcara, 1845), 28.6 × 16.0 mm, CS-PM, La Maddalena Isl., Sardinia, Italy, 1 m depth. **23, 24.** Details of shell sculpture. **26.** *Coralliophila meyendorffii*, detail of the larval whorls, specimen size 2.2 × 1.3 mm, CS-PM, La Maddalena Isl., Sardinia, Italy, 1 m depth. Scale bars = 1 cm, except for Figures 21, 26, scale bars = 200 µm.

species in the genus *Coralliophila* s. l., as traditionally formulated (see also Oliverio, in press). The new species was collected in Galicia together with the Atlantic-Mediterranean *Coralliophila squamosa* (Bivona, 1838). This latter species is generally collected in the Mediterranean Sea at depths ranging from 100 to 600 m (Figures 9–10). The new taxon is clearly conchologically distinguishable from all other eastern Atlantic and Mediterranean species of Coralliophilinae. *Coralliophila trigoi* shows a certain resemblance with the Mediterranean *Coralliophila panormitana* (Monterosato, 1869), but the latter is smaller, having a different sculpture that includes a larger number of spiral cords (22–24), with smaller scales (Figures 11–12).

Coralliophila trigoi is similar to *Coralliophila meyendorffii* (Calcara, 1845) (Figures 15–16, 22–26), but it differs by its more rounded shape, by having the length/width and length/aperture length ratios smaller (1.60 and 1.68 vs. 1.72 and 1.86), by possessing a larger number of primary spiral cords (15–20 vs. 13–15), which are narrower in width and differently sculptured, and by a reddish- or pale-brown color (*Coralliophila meyendorffii* is generally milky-white). Furthermore, the protoconch II of *Coralliophila trigoi* shows a number of whorls (2½) and a diameter (800 µm) different from the values on *Coralliophila meyendorffii* (3½ and 650–750 µm, respectively; see Figures 21, 26). The main shell morphological differences between these two species are summarized in Table 2. *Coralliophila meyendorffii* is a littoral, widely distributed species, occurring in the Mediterranean Sea (Figures 22–26), along the Atlantic African coast and Canary Islands (Figures 15–16). It is worth mentioning that *Coralliophila meyendorffii* preys on a variety of anthozoans, including the cnidarian *Calliactis parasitica* (personal observations). Interestingly, *Coralliophila trigoi* seems to be distributed along the Atlantic coast of Spain and Portugal, but restricted to the Alboran Sea (Malaga, Almeria) within the Mediterranean basin. The collecting depth is slightly deeper (50 m) than the bathymetric range (littoral) of *Coralliophila meyendorffii*. Although the planktotrophic mode of development (as indicated by the protoconch) of *Coralliophila trigoi* could bring about a wider geographic distribution than that currently known for the species, the taxon has not yet been found in the Macaronesian Islands and the West African coast.

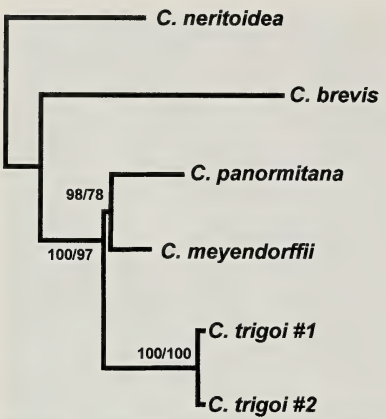


Figure 27. Cladogram of parsimony analysis for the studied coralliophiline taxa. This topology was recovered under maximum parsimony analysis of the 12S + ITS2 dataset (either including or excluding gap positions). Numbers at the branch represent bootstrap support in MP analyses (gap included and gaps as missing). Locality data and GenBank accession numbers (12S and ITS2) are reported in Table 1.

Coralliophila trigoi has been previously misidentified as *Coralliophila basilea* (Rolán, 1983: 236, fig. 210; Rolán, López and Gutiérrez-Garcia, 1995: 30, fig.2), but it is easily distinguishable from this taxon. *Coralliophila basilea* has a more turreted shell and a coarser spiral sculpture. Among the fossil coralliophiline records, the only species that slightly resembles the new taxon is *Coralliophila burdigalensis* (Tournouër, 1874), a species from the Upper Oligocene and Lower Miocene of Aquitaine (France); but the fossil species is smaller and has a different shell outline and sculpture (Lozouet and Renard, 1998: 173, figs. 2. 1–10).

Parsimony analysis of the aligned sequences of nuclear and mitochondrial DNA resulted in the tree reported in Figure 27. Accordingly, the two related species *C. meyendorffii* and *C. panormitana* were more closely related to each other than to the two specimens of the new species. The same results (not shown here) were obtained including additional (yet shorter) sequences of *C. meyendorffii* from other Mediterranean localities (Sardinia, Sicily, and Southern Spain). This is a clear indication that the specimens of the new form constitute a distinct, isolated gene-pool and strongly support our decision to describe it as new.

Table 2. Comparison of shell characters between *Coralliophila trigoi* and *C. meyendorffii*.

Shell characters	*C. trigoi*	*C. meyendorffii*
Protoconch diameter	800 μm	650–750 μm
Protoconch number of whorls	2.5	3.5
Teleoconch primary spiral cords	15–20	13–15
Teleoconch axial ribs	7–11	8–10
Length/width ratio	1.60 ± 0.09	1.72 ± 0.09
Length/aperture length ratio	1.68 ± 0.10	1.86 ± 0.10
Size range	17.6–35.4 mm	19.5–34.3 mm

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Book Review

Land Snails of British Columbia

Forsyth, Robert G. 2004. Land Snails of British Columbia. Royal BC Museum Handbook. Royal BC Museum, Victoria, 192 pp. ISBN 0-7726-5218-X. Black and white illustrations, plus a section of color photographs.

Even as "cutting edge" systematics shifts its focus from morphological to molecular data sets, the need for identification manuals based on real-world field marks and accessible characters has never been greater. When zoologists with landcare agencies or environmental consultants ask for references on land snails, it hardly helps to refer them to ponderous, outdated, and hard to find tomes such as Pilsbry (1939–1948). So, manuals like *Land Snails of British Columbia* are a welcome resource.

Land Snails of British Columbia is the latest in a Royal BC Museum series of natural history books that began in 1942. It is the first work to describe and illustrate the 92 species of terrestrial mollusks known to occur in British Columbia, Canada. Because all of the species treated occur outside that province as well, its utility extends beyond those borders. Identification aids include a paragraph of physical description, usually brief, to the point, and adequate; a sentence or two of comparison with other, potentially confusing species; clear illustrations (the line-and-stipple drawings of many of the smaller kinds are noteworthy); and keys to, first, the genera of snails and slugs, and then to the species in each multi-species genus. For slugs, where the diagnostic characters are often internal, excellent, predominantly original, drawings of the distal genitalia are provided. (The simple dissection needed to access these features should be within the range of all to whom this book is directed.) The language of the descriptions is simple and intelligible, and a glossary of technical terms is included. The descriptive material is followed by a summary of each species' distribution, concise comments on natural history, etymology of the generic and specific name, remarks that, among other things, update the species' taxonomic history (e.g., since Pilsbry, 1939–1948) or point out special conservation status, and selected references pointing to the extensive and well researched bibliography. All of this adds up to a highly functional volume that will serve its intended audience well.

A six-page section of color photographs of living snails and slugs, mainly by Kristiina Ovaska, is not only attractive but also helpful, particularly in showing the *habitus* of living slugs, something not always well conveyed by drawings.

The information is amalgamated (the author's word) from published literature, his own observations, scientific collections, and personal communications with other workers. The distributions are based in part on unpublished records from the Royal BC Museum and other collections. Specific localities are not cited; three online resources by the same author (Forsyth, 1999, 2005a, 2005b) provide more detail for specific regions.

A significant innovation is the introduction of *Euconulus* (*Euconulus*) *praticola* (Reinhardt, 1883) to the North American fauna. Its distinctness from *E.* (*E.*) *fulvus* (Müller, 1774) is well documented by characters of shell and external anatomy. The former catchall "Zonitidae" is correctly parsed into Pristilomatidae, Gastrodontidae, and Daudebardiidae for regional genera, in keeping with recent work by Hausdorf and others. *Monadenia*, iconic of northwest American forests, is correctly assigned to Bradybaenidae rather than the redundant and poorly argued Monadeniidae of Nordsieck (1987) and Schileyko (1996). In these and other ways, the author shows himself to be well "booked up" on the current and evolving literature of land snail systematics.

Overall, the taxonomy is simplified, appropriately for a general interest manual. Synonyms are merely listed, not referenced, as few potential users will need that entry into the primary literature. Subspecies are treated in the remarks, not in the major taxon headings or in the taxonomic checklist (pp. 23–28). If experience in California is any guide, upon further study some—perhaps most—nominal subspecies will be shown to be species; and examination of data not available to prior monographers may uncover local endemics, possibly in former glacial refugia such as the Queen Charlotte Islands. For the present, however, this handbook provides a reliable source of biodiversity information. Author Forsyth is fully aware of the dynamic character of taxonomic analysis and astutely states (p. 2), "this book is a work in progress." By clearly showing the state of our knowledge at this time, he has contributed greatly to that process.

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CONTENTS

Ellen E. Strong — A morphological reanalysis of *Pleurocera acuta* Rafinesque, 1831, and *Elimia livescens* (Menke, 1830) (Gastropoda: Cerithioidea: Pleuroceridae) 119

Richard L. Squires
LouElla R. Saul — New Late Cretaceous (Santonian and Campanian) gastropods from California and Baja California, Mexico 133

M. G. Harasewych
Yuri I. Kantor — *Daffymitra lindae*, a new genus and species of Volutomitridae (Neogastropoda) from the Bellingshausen Abyssal Plain 149

Sven N. Nielsen — *Exilia alanbeui*, a new species from the Neogene of central Chile: the first record of *Exilia* (Gastropoda: Ptychatractidae) from South America 153

Patricia Miloslavich
Ana Karinna Carbonini
Juan Manuel Díaz
Néstor E. Ardila — Spawn of *Amphissa* sp. and *Cosmioconcha* sp. (Caenogastropoda: Columbellidae) from the Colombian Caribbean 157

Thomas J. DeVries — *Pterorytis pacanana* new species (Gastropoda: Muricidae): circumstantial evidence for late Pliocene El Niño events in southern Peru 164

Eliézer de Carvalho Rios
Luiz Ricardo L. Simone — A new species of *Falsimargarita* (Gastropoda: Vetigastropoda: Trochidae) from the South Atlantic Ocean 169

Erratum 163

Notices 173, 174

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NATIONAL ENDOWMENT FOR THE ARTS

A morphological reanalysis of *Pleurocera acuta* Rafinesque, 1831, and *Elimia livescens* (Menke, 1830) (Gastropoda: Cerithioidea: Pleuroceridae)

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ABSTRACT

Pleurocera acuta and *Elimia livescens* have been the subject of several anatomical and ecological studies and are two of the most thoroughly documented species of North American Pleuroceridae. Yet significant gaps still remain in our understanding of their structure. Consequently, the anatomy of these two species is re-described, allowing a re-interpretation of pallial oviduct homologies; features not previously portrayed in the literature (midgut and kidney) are newly described. These taxa are characterized by the presence of an ovipositor, a kidney with a subdivided internal lumen that invades the pallial roof, a prostate with a highly folded anterior spermatophore-forming region, and a pallial oviduct with spermatophore bursa but lacking a seminal receptacle. This analysis verifies the degree of similarity between the two species, but a number of differences were identified including features of the ovipositor, pallial oviduct, prostate, anterior esophagus, midgut, kidney, pericardium and nervous system. Comparison to other pleurocerids confirms that species distributed in Western North America (*Juga*) and Asia (*Hua, Semisulcospira*) share the presence of a seminal receptacle—a feature that is lacking in all described Eastern North American species.

INTRODUCTION

The freshwater Pleuroceridae Fischer, 1885, comprises one of the most species-rich assemblages of limnic mollusks occurring in North America and Eastern Asia. In North America, they are represented by eight genera (*Athearnia* Morrison, 1971, *Elimia* H. and A. Adams, 1854, *Io* Lea, 1831, *Juga* H. and A. Adams, 1854, *Leptoxis* Rafinesque, 1819, *Lithasia* Haldeman, 1840, *Pleurocera* Rafinesque, 1818, and the extinct *Gyrotoma* Shuttleworth, 1845) and estimates of 159 species currently considered valid; of these, 34 are extinct and 59 are listed as critically imperiled (G1) or imperiled (G2) (Johnson et al., 2005).

The current concept of the family Pleuroceridae (e.g. Bouchet and Rocroi, 2005) can be traced to the works of Thiele (1928, 1929) who recognized 6 subfamilies within the heterogeneous "Melaniidae" (an invalid name for Thiaridae Gill, 1871), including the Pleurocerinae. An alternative, highly polyphyletic view promoted by Morrison (1954) caused great confusion for more than four decades concerning the extension and independence of the Pleuroceridae and Pachychilidae P. Fischer and Crosse, 1892 (e.g. Ponder and Warén, 1988). Recent work on the systematics of limnic lineages within the Cerithioidea Fleming, 1822 (e.g. Glaubrecht, 1996, 1999; Köhler et al., 2004) has resolved some of this confusion and supports the distinctiveness of these families on both morphological and molecular grounds. However, molecular data (Lydeard et al., 2002) do not support monophyly of the Pleuroceridae as currently defined, but suggest that a clade of eastern North American species are more closely related to *Melanopsis* (Melanopsidae H. Adams and A. Adams, 1854) than to a clade of western North American (*Juga*) and eastern Asian pleurocerids (*Semisulcospira* Boettger, 1886, *Hua* Chen, 1943).

As noted by Woodard (1934), anatomical data are critical in refining the phylogenetic relationships and classification of these species. However, all taxonomic treatments of the family have been based primarily on conchological characters in the absence of a broad comparative understanding of morphology. Although the subject of numerous ecological studies (e.g. Dillon, 2000) and comparably many descriptions exist for the radula, operculum and life history of North American pleurocerids, surprisingly little is known about their basic biology and anatomy. Scant information on the anatomy (besides radula and operculum) has been provided for *Elimia laqueata* (Say, 1829) (Woodard, 1934), *E. potosiensis* (Lea, 1841) (Jones and Branson, 1964) and *Pleurocera canaliculata* (Say, 1821) (Magruder, 1935b); among western North American forms, only reproductive anatomy is known for several species (Prozorova and Raschepkina, 2004). In addition, the

classically cited work of Dazo (1965) on the natural history, ecology, distribution and anatomy of *Pleurocera acuta* Rafinesque, 1831 and *Elimia livescens* (Menke, 1830) has long stood as the most comprehensive morphological study of any pleurocerid gastropod. As such, that study has formed the basis for hypotheses of homology in recent higher-order phylogenetic studies based on morphology (e.g. Houbrick, 1988; Glaubrecht, 1996). Yet, Dazo's study was completed long before our present understanding of the structure, function and homologies of cerithioidean reproductive anatomy was in place, particularly through the work of R. S. Houbrick on marine species. We also have a much more thorough understanding of midgut structure and its utility in revealing phylogenetic affinities of cerithioideans (Glaubrecht and Strong, 1999; Strong and Glaubrecht, 1999, unpublished data).

Given the persistent paucity of anatomical data available for the family, the goal of this contribution is to reevaluate the morphology and putative homologies of the two species described by Dazo, and to place them within the emerging framework now available for limnic cerithioideans. This is critical for ongoing morphological and phylogenetic studies of cerithioidean gastropods, and in particular for clarifying the monophyly and systematic affinity of the family Pleuroceridae.

MATERIALS AND METHODS

This study is based on collections of individuals of *Pleurocera acuta* and *Elimia livescens* living sympatrically in the Mukwonago River at the outflow from Lower Phantom Lake, Mukwonago, Waukesha County, Wisconsin (42°51.402 N; 88°19.767 W). Populations were sampled in May and June; only reproductively mature individuals were used for observations of reproductive anatomy. Individual specimens were cracked, preserved in 95% ethanol and were not relaxed. Voucher material is deposited in the National Museum of Natural History in Washington (USNM).

As stated above, Dazo (1965) provided a rather detailed account of external features (operculum, shell, ovipositor, color patterns of the head-foot) as well as of the radula and all internal organ systems (alimentary, nervous, excretory, respiratory, vascular, and reproductive systems). Baker (1928) also provided information on the operculum, jaw, radulae, and external anatomy of the two species; additional scattered accounts relating to the radula, external anatomy and life history are also available (e.g. Jewell, 1931; Howe, 1938; Goodrich, 1945). As such, the following reanalysis emphasizes anatomy of the soft parts. As the two species are overwhelmingly similar, a thorough account is provided for *Pleurocera acuta* – the type species of the type genus for the family; only details that differ are noted for *Elimia livescens*. However, the internal kidney structure of *P. acuta*, while displaying the same configuration as *E. livescens*, is too occluded with excretory tissue to allow a clear representation. As such, only the internal structure for the latter species is illustrated.

Specimens were examined using a Leica MZ 12,5 binocular microscope with camera lucida; visualization of structures was enhanced through the use of aqueous toluidine blue. Typically four to five specimens were examined for each organ system investigated, especially for those systems showing high levels of individual and/or seasonal variation (i.e. reproductive system); a minimum of two individuals were examined for particularly complex structures (i.e. midgut, nerves). Descriptions of midgut morphology are given with the stomach opened dorsally and the style sac uppermost. Unless otherwise indicated, an incision is made along the extreme right, upper and lower margins, and the roof deflected laterally to the left. Terminology follows Strong and Glaubrecht (2002, 2003).

RESULTS

Pleurocera acuta Rafinesque, 1831

Material Examined: Wisconsin: Mukwonago River: USNM 1081522, 1081524.

External Anatomy: Operculum sub-ovate, corneous, dark reddish-brown in color, with 3.5 whorls; paucispiral with large, eccentric nucleus of approximately 2.75 to 3 whorls (Figure 1). Final whorl moderately inflated. Nucleus occupying slightly under 1/2 (~43%) of total length.

Foot ovate with narrow propodium; anterior pedal gland opening along anterior margin (Figure 2, **ap**). Ovipositor (**ovp**) located on side of neck below right cephalic tentacle. Ciliated egg groove extending short distance up side of neck from ovipositor, shallowing past mantle margin; groove fading near anal aperture. Two, partially juxtaposed, parallel folds, extending into ovipositor pore from aperture (*); one fold at upper posterior edge, second at lower anterior edge of ovipositor (when viewed laterally), forming obliquely flattened H-shaped lumen. Folds unequal in size; anterior fold along floor significantly larger than posterior fold along roof. Ovipositor pore expanding medially into head-foot, then curving and narrowing slightly posteriorly. Two vertical limbs of "H" unequal such that posterior limb forming rather narrow channel along posterior wall. Anterior limb inflated and expanding medially into foot, forming large flattened, subtriangular chamber. Folds diminishing toward blind tip of pore. Short grooved tract extending ventrally from ovipositor aperture toward foot sole, but not reaching edge of foot.

Most individuals with straight osphradium, but some with curved anterior tip (Figure 3, **os**). Hypobranchial gland highly developed with pendulous, transverse folds (Figure 4, **hg**).

Alimentary System: Foregut. Buccal mass short and stout, extending to base of cephalic tentacles (Figure 3,

Figures 1–4. Anatomy of *Pleurocera acuta*. **1.** Operculum. **2.** Ovipositor and egg groove. Right lateral view of side of foot. Asterisks (*) indicate folds extending into ovipositor. **3.** Mantle cavity and anatomy of cephalic hemocoel. Dorsal view, anterior is below. Hypobranchial gland removed for clarity. **4.** External view of organs in visceral mass. Dotted line indicates extent of pericardium under main kidney chamber. Abbreviations: **ap,** anterior pedal gland; **b,** bladder; **bm,** buccal mass; **cm,** columellar muscle; **ct,** ctenidium; **e,** esophagus; **hg,** hypobranchial gland; **int,** intestine; **kd,** main kidney chamber; **me,** mantle edge; **nr,** circum-esophageal nerve ring; **op,** operculum; **os,** osphradium; **ov,** ovary; **ovp,** ovipositor; **per,** pericardium; **po,** pallial oviduct; **ps,** peri-intestinal sinus; **r,** rectum; **rt,** buccal mass retractor muscle; **sg,** salivary gland; **sn,** snout; **sp,** supra-esophageal ganglion; **ss,** style sac; **sto,** stomach. Scale bars = 1 mm.

bm). Odontophore occupying majority of buccal cavity with small, glandular subradular organ protruding before radula. Small jaws present at anterior ends of dorsal folds; epithelium of buccal cavity overlying dorsal folds glandular (stippled region). Shallow, non-glandular buccal pouches extending underneath dorsal folds adjacent to buccal ganglia at rear of buccal cavity. Radular sac short, curving upward behind base of buccal mass. Robust buccal retractors (**rt**) inserting onto lateral walls of cephalic hemocoel adjacent to cerebral ganglia (**nr**). Short, glandular mid-ventral fold forming small flap just behind odontophore in anterior esophagus, flanked laterally by two ventro-lateral folds. Ventro-lateral folds converging short distance behind mid-ventral fold and continuing through mid-esophagus (**e**). Mid-esophagus long, bearing paired longitudinal ventral and dorsal folds. Epithelium between dorsal and ventral folds weakly glandular and irregularly striated; septate esophageal gland lacking. Dorsal and ventral folds converging and fusing at distal end of mid-esophagus before continuing into posterior esophagus and subdividing into numerous folds equal in height. Long, tubular salivary glands (**sg**) opening dorso-laterally to buccal cavity alongside odontophore, passing through circum-esophageal nerve ring (**nr**), almost reaching posterior esophagus.

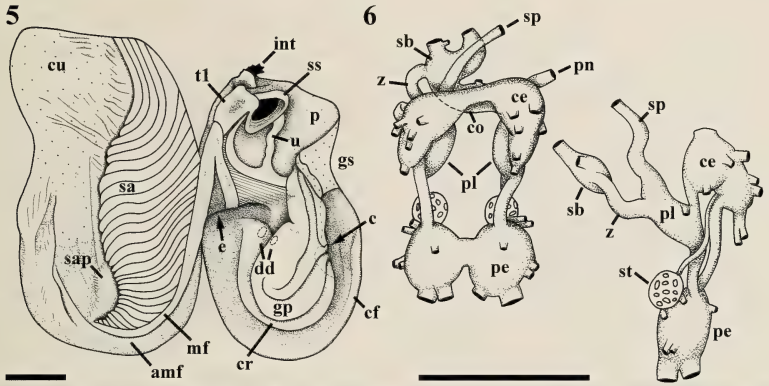
Midgut. Esophagus opening under ledge on left side of midgut floor (Figure 5, **e**). Marginal fold (**mf**) extending anteriorly from esophageal aperture alongside major typhlosole (**t1**), then turning posteriorly bordering right margin of sorting area (**sa**). Groove present along midline of marginal fold (**mf**) for much of its length; groove fading proximally and distally. Sorting area elongate- triangular, tapering posteriorly; posterior tip curving slightly to the left around wedge-shaped sorting area pad (**sap**). Accessory marginal fold (**amf**) emerging from esophageal aperture, paralleling marginal fold and curving around posterior tip of sorting area; fold bifurcating at posterior end of gastric chamber to form two folds. Fine parallel striations extending anteriorly from esophagus up face of major typhlosole. Midgut roof to the left of sorting area coarsely folded and cuticularized (**cu**). Gastric shield (**gs**) small and delicate, strongly concave, with narrow, tubular posterior end and more flaring, flattened anterior end; shield continuous with cuticle of stomach roof and crystalline style pocket (**p**). Glandular pad (**gp**) large and broadly rounded. Crescentic ridge (**cr**), bounding deep crescentic groove, extending from esophageal aperture and fusing to right side of glandular pad. Paired digestive gland ducts (**dd**) opening to deep pocket near proximal tip of crescentic ridge. Shallow caecum (**c**) extending ventrally under glandular pad behind gastric shield. Single longitudinal fold (**cf**) extending from caecum (**c**) around posterior end of gastric chamber. Prominent fold (**u**) extending from right side of style sac lip, along floor of crystalline style pocket, to base of major typhlosole; fold bounding u-shaped depression below lip of style sac (**ss**). Style sac and intestinal groove communicating along entire length. Crystalline style present.

Hindgut. Proximal intestine (Figure 4, **int**) passing below distal tip of style sac (**ss**), then extending posteriorly alongside style sac to main gastric chamber (**sto**). Intestine curving anteriorly, with broad loop overlying proximal style sac. Intestine extending under posterior end of main kidney chamber (**kd**), entering pallial roof alongside bladder (**b**) and pallial gonoduct (Figure 3, **po**), continuing forward to papillate anus near mantle margin (**r**).

Reno-pericardial System: Kidney comprising three interconnected chambers (Figure 4, 17, **kd**, **b**). Main chamber (**kd**) lying along dorsal surface of body whorl, anteriorly surrounding pericardium (Figure 4, **per**), crossing axis of body from right to left and extending short distance into pallial roof at base of mantle cavity. Chamber occluded anteriorly (within pallial roof) with excretory tubules. Posteriorly, main chamber with small, narrow lumen, dorsally enclosing intestine. Second chamber (see exposed chamber in Figure 17) extending between pericardial chamber to right body wall below intestine, forming small bladder (Figure 4, **b**). Chamber mostly occluded by vertical sheets of excretory tissue radiating from afferent renal vessel (see Figure 17, **arv**), and communicating to mantle cavity via large nephropore (**np**). Sheets of excretory tissue branching and anastomosing, and fusing to right lateral floor, roof and walls; vertical sheets highly branched anteriorly and forming comparatively dense honeycomb of excretory tissue. Bladder penetrating connective tissue along right side of body, short distance into mantle roof. Excretory tissue separating small ventral chamber below, within pallial portion (dotted line). Size of ventral chamber, as well as branching pattern and number of excretory sheets of tissue variable between individuals. Small aperture just behind afferent renal vessel connecting main chamber and bladder (arrow). Nephridial gland absent.

Pericardium voluminous (Figure 4, **per**), extending to right side of body (dotted line).

Nervous System: Circum-esophageal nerve ring (Figure 3, **nr**) lying immediately behind buccal mass, at base of cephalic tentacles. Cerebral ganglia (Figure 6, **ce**) connected by short, stout commissure, each producing seven nerves (optic, statocyst, tentacular, and four labial nerves). Buccal connectives short, innervating buccal ganglia lying ventro-laterally at base of buccal cavity immediately behind buccal retractor muscles. Pleural ganglia (**pl**) lying behind and below cerebral ganglia connected to cerebral ganglia by short, thick connectives. Pedal ganglia (**pe**) with two prominent anterior nerves and five smaller accessory nerves. Small statocysts (**st**) with approximately 10–15 statoconia present dorsally alongside pedal ganglia behind pedal connectives. Sub-esophageal ganglion (**sb**) joined to left pleural ganglion by thickened connective (**co**); connec-

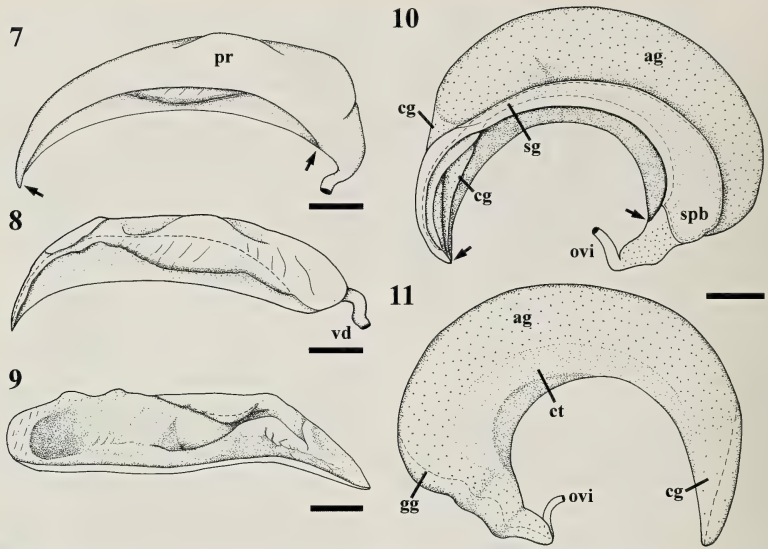


Figures 5–6. Anatomy of *Pleurocera acuta*. **5.** Midgut anatomy. Dorsal view, anterior is uppermost. **6.** Circum-esophageal nerve ring. Frontal view on the left, right lateral view on the right. Abbreviations: **amf,** accessory marginal fold; **c,** caecum; **cf,** caecal fold; **ce,** cerebral ganglion; **co,** thickened connective between left pleural and sub-esophageal ganglia; **cr,** crescentic ridge; **cu,** cuticularized region of stomach roof; **dd,** duct of digestive gland; **e,** esophageal aperture; **gp,** glandular pad; **gs,** gastric shield; **int,** intestine; **mf,** marginal fold; **p,** crystalline style pocket; **pe,** pedal ganglion; **pl,** pleural ganglion; **pn,** pallial nerve from left pleural ganglion; **sa,** sorting area; **sap,** sorting area pad; **sb,** sub-esophageal ganglion; **sp,** connective to supra-esophageal ganglion; **ss,** lip of style sac; **st,** statocyst; **t1,** major typhlosole; **u,** u-shaped fold; **z,** zygoneury. Scale bars = 1 mm.

tive producing 1–3 small nerves (n=2). Zygoneury (**z**) formed between sub-esophageal and right pleural ganglia. In addition to zygoneury (**z**), sub-esophageal ganglion (**sb**) producing one other prominent nerve and connectives to the left pleural (**pl**) and visceral ganglia. Long connective uniting right pleural and supra-esophageal ganglia (Figures 3, 6, **sp**), the latter lying on left side mantle floor near midline of osphradium. Dialyneury formed between pallial nerve of left pleural ganglion and osphradial nerve of supra-esophageal ganglion at junction of mantle roof and floor. Single visceral ganglion present between pericardium and kidney at base of mantle cavity, above posterior esophagus on the right. Ganglion producing two prominent nerves.

Reproductive System: Male. Narrow vas deferens (Figure 8, **vd**) emerging ventrally from testes, continuing forward along ventral midline of whorl. Short, distal portion of vas deferens thickened and forming straight seminal vesicle. Vas deferens narrowing and curving dorsally to enter posterior end of prostate (Figure 7, **pr**) at base of mantle cavity. Prostate glandular, forming flattened tube, opening to mantle cavity through broad slit along entire length except for a short fused segment at base of mantle cavity (arrows). Lateral lamina epithelium thin along aperture; short distance into lumen, glandular tissue forming flattened longitudinal shelf. Glandular tissue diminishing in thickness at anterior and posterior ends of gonoduct. Shelf undercut along much of its length by flattened sinus (Figure 8, dotted line). Glandular tissue forming central rounded mass flanked by shallow trough along gonoductal groove. Medial lamina unevenly glandular, with irregular troughs and ridges; glandular tissue diminishing in thickness anteriorly and posteriorly (Figure 9). Epithelium of medial lamina posterior 1/5 smooth and concave, partially separated from anterior region by prominent curving ridge; ridge embracing corresponding rounded glandular mass in lateral lamina. Ridge continuous anteriorly with curving trough formed by opposing ridges of tissue. Trough fading anteriorly, and becoming flanked by short, shallow flap running along gonoductal groove.

Female. Gonad (Figure 4, **ov**) dorsally surrounding digestive gland (except for a narrow ventral strip) from tip of visceral mass to posterior end of midgut (**sto**). Oviduct emerging ventrally from ovary. Renal oviduct (Figures 10, 11, **ovi**) deflected dorsally behind mantle cavity before entering base of glandular pallial oviduct. Pallial oviduct, with proximal albumen (**ag**) and distal capsule glands (**cg**). Albumen and capsule glands forming narrow bands with opposing flattened surfaces bounding gonoductal groove (Figure 11, **gg**); non-glandular portions of medial and lateral laminae formed by thickened connective tissue (**ct**). Proximal segment of albumen gland at base of mantle cavity under pallial kidney extension rather short and straight (Figures 10,



Figures 7–11. Reproductive anatomy of *Pleurocera acuta*. **7.** External, left lateral view of prostate. Anterior is to the left. Arrows indicate extent of opening to gonoductal groove. **8.** Internal aspect of prostate lateral lamina. Dotted line designates extent of sinus under glandular shelf. **9.** Internal aspect of prostate medial lamina. Anterior is to the right. Note parallel folds and groove at anterior end, representing presumptive spermatophore forming region. **10.** External, left lateral view of pallial oviduct. Anterior is to the left. Arrows indicate extent of opening to gonoductal groove. **11.** External, right lateral view of pallial oviduct. Anterior is to the right. Abbreviations: **ag,** albumen gland; **cg,** capsule gland; **ct,** connective tissue; **gg,** gonoductal groove; **ovi,** renal oviduct; **pr,** prostate; **sg,** sperm gutter; **spb,** spermatophore bursa; **vd,** vas deferens. Scale bars = 1 mm.

11, **ag**). Anterior to pallial kidney chamber, albumen gland curving under distal tip of bursa to the right, then arcing dorsally. Capsule gland comprising approximately anterior 1/4 of pallial oviduct; externally capsule gland not inflated (Figure 10, **cg**). Broad aperture along entire length of pallial oviduct except for a short fused segment at base of mantle cavity (Figure 10, arrows). Above aperture, sperm gutter (**sg**) opening in medial lamina at anterior tip of pallial oviduct and deepening posteriorly; gutter leading to short, blind spermatophore bursa (**spb**). Seminal receptacle absent.

Elimia livescens (Menke, 1830)

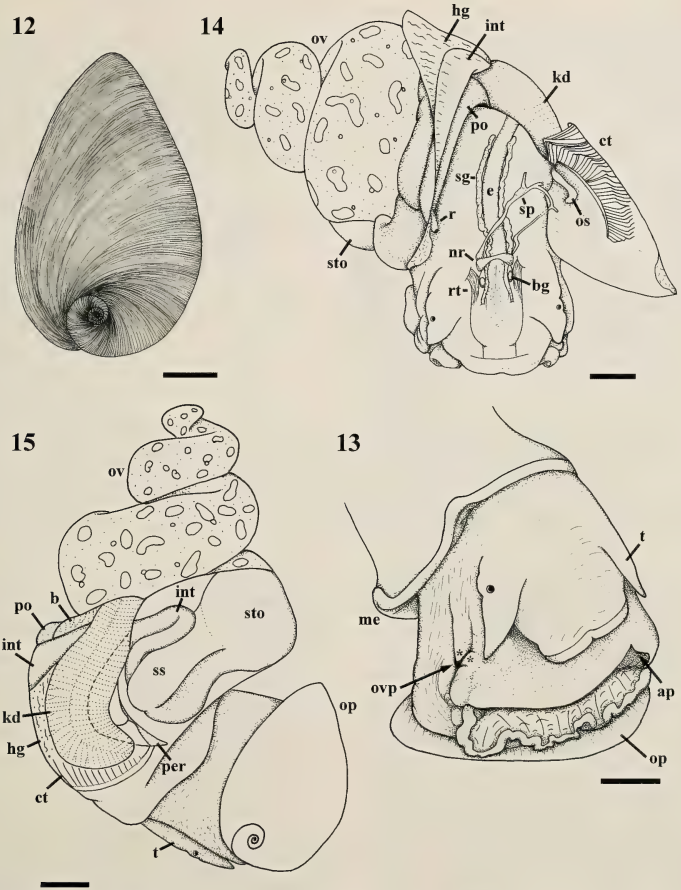
Material Examined: Wisconsin: Mukwonago River: USNM 1081521, 1081523.

External Anatomy: Operculum ovate, corneous, dark reddish-brown in color, with three whorls; paucispiral with small, basal nucleus of approximately 2.5 whorls (Figure 12). Last whorl expanding rapidly. Nucleus comprising approximately 1/5 of total length.

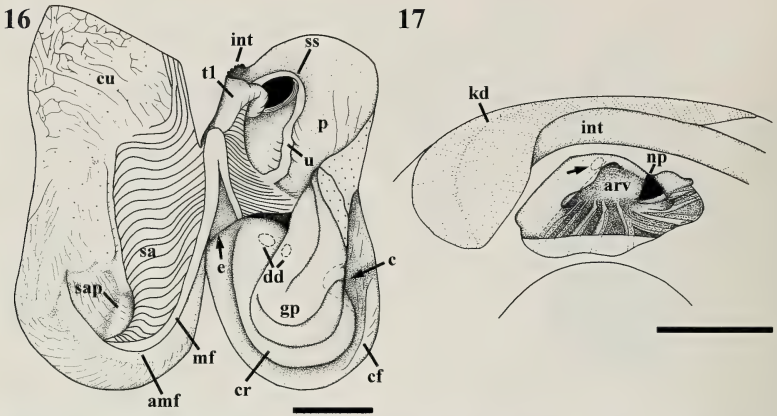
Foot broad and rounded, with wide propodium and long anterior pedal gland along anterior margin (Figure 13, **ap**). Ciliated egg groove extending short distance up side of neck from ovipositor; groove fading near base of tentacle. Parallel folds extending into ovipositor pore from aperture (*) roughly equal in size. Grooved tract extending ventrally from ovipositor to sole of foot at junction of propodium and mesopodium, just behind termination of anterior pedal gland.

Osphradium with curved anterior tip; some individuals with mostly straight osphradium (Figure 14, **os**). Hypobranchial gland well developed with deep, transverse folds (Figures 14, 15, **hg**).

Alimentary System: FOREGUT. Epithelium between dorsal and ventral folds glandular and irregularly to transversely striated. Dorsal and ventral folds diminish-



Figures 12–15. Anatomy of *Elimia livescens*. **12.** Operculum. **13.** Ovipositor and egg groove. Right lateral view of side of foot. Asterisks (*) indicate folds extending into ovipositor. **14.** Mantle cavity and anatomy of cephalic hemocoel. Dorsal view, anterior is below. **15.** External view of organs in visceral mass. Dotted line indicates extent of pericardium under main kidney chamber. Abbreviations: **ap,** anterior pedal gland; **b,** bladder; **bg,** buccal ganglion; **ct,** ctenidium; **e,** esophagus; **hg,** hypobranchial gland; **int,** intestine; **kd,** main kidney chamber; **me,** mantle edge; **nr,** circum-esophageal nerve ring; **op,** operculum; **os,** osphradium; **ov,** ovary; **ovp,** ovipositor; **per,** pericardium; **po,** pallial oviduct; **r,** rectum; **rt,** buccal mass retractor muscle; **sg,** salivary gland; **sp,** supra-esophageal ganglion; **ss,** style sac; **sto,** stomach; **t,** cephalic tentacle. Scale bars = 1 mm.



Figures 16–17. Anatomy of *Elimia livescens*. **16.** Midgut anatomy. Dorsal view, anterior is uppermost. **17.** Kidney anatomy. Internal view of bladder. Lateral view, anterior is to the right. Right wall of bladder and adhering sheets of excretory tissue removed to reveal interior; cross-hatching indicates cross-section through sheets of tissue. Arrow indicates opening in septum allowing communication between bladder and main kidney chamber. Dotted line anteriorly indicates extent of ventral chamber. Abbreviations: **amf,** accessory marginal fold; **arv,** afferent renal vessel; **c,** caecum; **cf,** caecal fold; **cr,** crescentic ridge; **cu,** cuticularized region of stomach roof; **dd,** duct of digestive gland; **e,** esophageal aperture; **gp,** glandular pad; **gs,** gastric shield; **int,** intestine; **kd,** main kidney chamber; **mf,** marginal fold; **np,** nephropore; **p,** crystalline style pocket; **sa,** sorting area; **sap,** sorting area pad; **ss,** lip of style sac; **t1,** major typhlosole; **u,** u-shaped fold. Scale bars = 1 mm.

ing at distal end of mid-esophagus (Figure 14, **e**) but continuous into posterior esophagus. Posterior esophagus narrow, bearing numerous folds of equal height. Long, tubular salivary glands (**sg**) just reaching transition to posterior esophagus.

Midgut. Groove along midline of marginal fold lacking (Figure 16, **mf**). Single, weak, caecal fold (**cf**) along right side of midgut behind gastric shield, opposite caecum.

Hindgut. Proximal intestine (Figure 15, **int**) passing below distal tip of style sac (**ss**), then extending posteriorly alongside style sac almost reaching main gastric chamber (**sto**). Intestine curving anteriorly with loop partially overlying proximal style sac. Intestine extending under posterior end of main kidney chamber (**kd**), entering pallial roof alongside bladder (**b**) and pallial gonoduct (**po**), continuing forward to papillate anus near mantle margin (Figure 14, **r**).

Reno-pericardial System: Bladder (Figure 15, **b**) largely occluded by vertical sheets of excretory tissue radiating from afferent renal vessel (Figure 17, **arv**) and fusing to right lateral floor, roof and walls. Sheets of excretory tissue loosely and regularly branching and anastomosing; posterior sheets less branched than those anteriorly.

Pericardium rather narrow and short (Figure 15, **per**), extending to intestinal loop (dotted line).

Nervous System: Buccal ganglia (Figure 14, **bg**) lying dorso-laterally at base of buccal mass between buccal retractor muscles (**rt**) and salivary glands (**sg**). Thickened connective (Figure 18, **co**) between left pleural and sub-esophageal ganglia producing 1–2 nerves (n=2). In addition to zygoneury (**z**) and connectives to left pleural and visceral ganglia, sub-esophageal ganglion producing 2–3 prominent nerves (n=2). Small statocysts (**st**) with approximately 20–30 statoconia.

Reproductive System: Male. Flattened longitudinal shelf of glandular tissue within lateral lamina diminishing in thickness at anterior and posterior ends of prostate (Figures 19, 20, **pr**). Deep longitudinal cleft opening in glandular shelf along gonoductal groove at midpoint of gonoduct and extending anteriorly; cleft closing a short distance back from anterior tip of gonoduct (Figure 20, **cl**). Medial lamina thinly and rather evenly glandular along its length; glandular tissue slightly diminishing anteriorly (Figure 21). Epithelium of medial lamina posterior third smooth and strongly concave, separated from anterior 2/3 by prominent curving ridge; ridge embracing corresponding groove in glands of lateral lamina at proximal end of cleft. Epithelium of medial lamina anterior 2/3 irregularly and variably crossed by oblique and longitudinal ridges.

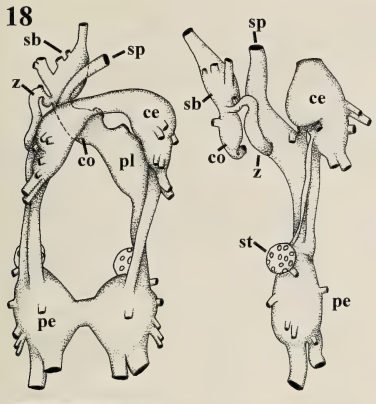


Figure 18. Circum-esophageal nerve ring of *Elimia livescens*. Frontal view on the left, right lateral view on the right. Abbreviations: **ce,** cerebral ganglion; **co,** thickened connective between left pleural and sub-esophageal ganglia; **pe,** pedal ganglion; **pl,** pleural ganglion; **sb,** sub-esophageal ganglion; **sp,** connective to supra-esophageal ganglion; **st,** statocyst; **z,** zygoneury. Scale bar = 1 mm.

Female. Renal oviduct (Figures 22, 23, **ovi**) deflected dorsally behind mantle cavity before entering base of glandular pallial oviduct. Proximal albumen gland rather long and initially curved, then forming straight segment along base of mantle cavity under pallial kidney extension. Capsule gland comprising approximately anterior 1/3 of pallial oviduct; externally capsule gland markedly inflated. Above aperture, short distance back from anterior tip of oviduct (~1/5 of length), sperm gutter (**sg**) opening in medial lamina and deepening posteriorly; gutter leading to short, blind spermatophore bursa (**spb**).

DISCUSSION

Whatever may be discovered in the future regarding the structure and relationships of species currently placed within the Pleuroceridae, given that *Pleurocera acuta* is the type species of the type genus for the family, this description will necessarily remain as the standard for the application of the name.

Comparison of *Pleurocera acuta* and *Elimia livescens*

Baker (1928) commented on the considerable uniformity of structure in the genitalia of these two species and that the soft parts do not seem to show the same degree of differentiation as the shells. Although this statement was based on external observations, Dazo (1965) similarly noted that, except for differences in size, the internal anatomy of the two species is quite similar or often identical in all organ systems; the most significant differences were those relating to size and shape of the operculum, snout, tentacles, foot, and radula.

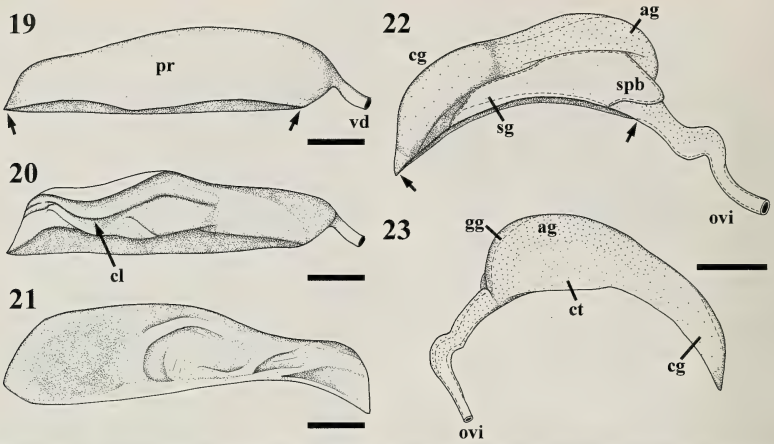
Yet, notions of similarity and how similar two entities must be to be characterized as "identical" are subjective concepts. The thorough documentation of these two species has been provided to allow a more objective means of assessing the degree of similarity between the two. Of course, any anatomical rendering will maintain some element of subjectivity.

With this in mind, the present analysis confirms that *Pleurocera acuta* and *Elimia livescens* are remarkably similar, both in overall organization and in many details. This level of similarity is perhaps not unexpected given the sister group relationship between the two genera supported in one molecular analysis (Holznagel and Lydeard, 2000). However, it should be noted that monophyly of these genera has not been demonstrated unambiguously (e.g. Sides, 2005), but awaits confirmation within a more comprehensive phylogenetic framework. Thus, the present results may indicate a closer systematic affinity than currently appreciated.

Yet, a number of differences between the two species are apparent. Externally, the two differ in development of the hypobranchial gland, but this is difficult to quantify. They also differ in the position of the ovipositor and its relationship to the foot sole. This is consistent with described differences in the mode of egg capsule transfer to the substrate; in *Pleurocera acuta*, only the everted walls of the ovipositor function in oviposition (van Cleave, 1932), but in *Elimia laqueata*—a species with an ovipositor configuration identical to *E. livescens* (see below)—both the everted lips of the ovipositor and the margins of the finely grooved tract guide the ova to the substrate (Woodard, 1934).

The most significant differences in midgut structure are length of caecal fold, and the presence of a groove along the marginal fold; however, these variations may be attributable to preservation artifacts. The significance of other minor differences (size and/or shape of caecum, glandular pad, major typhlosole, gastric shield, crescentic ridge, field of parallel striations above esophageal aperture) can only be ascertained once a broader sampling of species from both genera have been examined. But these may also be attributable to preservation artifacts and/or intra-specific variation.

Internal structure of the kidney differs only in that the vertical sheets of excretory tissue are more highly and densely branched within the bladder in *Pleurocera acuta*. It was observed that the amount of such excretory tissue varied between individuals in a species and with maturity. Although a highly qualitative character, the degree of difference between the two species surpasses that of intra-specific variation.



Figures 19–23. Reproductive anatomy of *Elimia livescens*. **19.** External, left lateral view of prostate. Anterior is to the left. Arrows indicate extent of opening to gonoductal groove. **20.** Internal aspect of prostate lateral lamina. Note deep cleft at anterior end (**cl**), representing presumptive spermatophore forming region. **21.** Internal aspect of prostate medial lamina. Anterior is to the right. **22.** External, left lateral view of pallial oviduct. Anterior is to the left. Arrows indicate extent of opening to gonoductal groove. **23.** External, right lateral view of pallial oviduct. Anterior is to the right. Abbreviations: **ag,** albumen gland; **cg,** capsule gland; **cl,** deep cleft; **ct,** connective tissue; **gg,** gonoductal groove; **ovi,** renal oviduct; **sg,** sperm gutter; **spb,** spermatophore bursa; **vd,** vas deferens. Scale bars = 1 mm.

The configuration of the nerve ring and visceral loop is largely identical between the two. One difference is the number of nerves issuing from the sub-esophageal/left pleural connective and from the sub-esophageal ganglion. However, given the observed intra-specific variation, these differences likely fall within the range of individual variation.

In contrast to the results presented here, Dazo (1965) reported 9 cerebral nerves, only a single nerve from the visceral ganglion, and an inconstant number of accessory pedal nerves; however, Dazo did confirm the unique thickened left pleural/sub-esophageal connective. Dazo also commented on the unlikely generality of Rosewater's (1961) findings that pleurocerids differ primarily in the lengths of the cerebral commissure and left pleural/sub-esophageal connective (n=6 for 9 species). Indeed, these lengths were found to be sometimes conspicuously different between individuals examined in the present study.

Males of the two species differed in the pattern of folds within the anterior region of the prostate. Regardless, the anterior region is inferred to be the site of spermatophore formation rather than the comparatively smoother posterior region. This conclusion seems justified given the similarity in the configuration of the folds as compared to overall form and shape of the spermatophore (Jewell, 1931; Dazo, 1965). Limnic cerithioideans in the family Paludomidae Stoliczka, 1868, have separated the glands in this anterior region to form a hollow tube that has been implicated in spermatophore formation (Glaubrecht and Strong, 2004). That discovery further supports the notion that sperm packets are produced anteriorly and suggests that this function may be homologous in different lineages.

For a summary of these and other morphological differences, see Table 1.

Comparison to Other Pleurocerids

With minor exception, published accounts agree on the main patterns of pleurocerid anatomy. Thus, pleurocerids have long been known to be dioecious and oviparous (except *Semisulcospira*) with an ovipositor involved in the deposition of the egg capsules (Stimpson, 1864). Members of the family are also aphallate, with open gonoducts, a gonad that dorsally surrounds the digestive gland, and produce crescent-shaped spermatophores (e.g. Stimpson, 1864; Jewell, 1931; Woodard, 1934, 1935; Magruder, 1935b; Jones and Branson, 1964; Dazo, 1965). Like other cerithioideans, pleurocerids possess

Table 1. Summary of morphological differences between *Pleurocera acuta* and *Elimia livescens*.

	Pleurocera acuta	*Elimia livescens*
External Anatomy:		
Propodium	Narrow	Broad
Ovipositor ventral groove	Does not extend to foot margin	Extends to foot margin
Curved anterior tip of osphradium	Sometimes present	Often present
Alimentary System:		
Ventral folds at posterior end of mid-esophagus	Fused	Unfused
Groove along marginal fold	Present	Absent
Length of caecal fold	Long	Short
Hindgut loop	Extends to main gastric chamber	Does not reach main gastric chamber
Reno-Pericardial System:		
Bladder excretory tubules	Densely and highly branched	Loosely and regularly branched
Pericardium	Extends to right body wall	Extends to intestinal loop
Nervous System:		
Buccal ganglia	Ventro-lateral	Dorsal
Statoconia	~10–15	~20–30
Nerves from sub-esophageal/left pleural connective	1–3	1–2
Nerves from sub-esophageal ganglion	2 connectives and 2 nerves (including zygoneury)	2 connectives and 3–4 nerves (including zygoneury)
Reproductive System:		
Spermatophore-forming region	Parallel folds and trough in medial lamina	Deep cleft in lateral lamina
Sperm gutter	Extends to anterior tip of oviduct	Does not extend to anterior tip of pallial oviduct
Junction of renal and pallial oviduct	Renal oviduct curves dorsally to straight segment of albumen gland	Renal oviduct ventrally joins curved portion of albumen gland
Proximal albumen gland	Short, straight segment between renal oviduct and posterior end of bursa	Initially curved, with long, straight segment to posterior end of spermatophore bursa

two types of glands within the pallial oviduct – a feature not previously documented among eastern North American species.

The gut is characterized by the presence of tubular salivary glands, a crystalline style and a style sac in restricted communication with the proximal intestine (Magruder, 1935a, b; Itagaki, 1960; Dazo, 1965). The bi-lobed nature of the kidney has been noted before (Magruder, 1935b; Itagaki, 1960), but the internal subdivision of the organ had not been previously documented.

The nervous system is consistent with many other cerithioideans (left dialyneurous, long connective between the right pleural and supra-esophageal ganglia, single visceral ganglion) (e.g. Strong, 2003; Strong and Glaubrecht, 2002, 2003), but is distinguished by the presence of an enlarged connective between the left pleural and sub-esophageal ganglia and a zygoneurous connection on the right—the latter a highly homoplastic character in the Cerithioidea (see review in Houbrick, 1988). However, the presence/absence of zygoneury among pleurocerids requires confirmation as it has been depicted as dialyneury in several other species (Magruder, 1935b; Itagaki, 1960). Only the former study confirmed the presence of the enlarged left pleural and sub-esophageal connective. Additionally, published descriptions (Magruder, 1935b; Itagaki, 1960; Dazo, 1965; present study) disagree on the number of nerves produced by various ganglia, but as noted above, this can be highly variable even within species. However, the number of statoconia reported by Magruder (30–40; 1935b) is significantly more than the number reported herein, possibly exceeding the level of intra-specific variation and, thus may be an informative phylogenetic character.

Several significant discrepancies among previous descriptions of pleurocerid anatomy are now resolved. Woodard (1934, 1935) observed a so-called "cytophore organ" at the base of the mantle cavity, apparently confluent with the sperm duct. Similarly, Dazo (1965) reported the presence of a cytophore organ in males of both *Pleurocera acuta* and *Elimia livescens*. Based on the present analysis and Woodard's description of the internal structure and position of this organ, it is clear that Woodard misidentified the kidney bladder as a part of the reproductive tract. However, it is not clear why the cytophore organ was described as lacking in females. The intimate connection between the bladder and proximal pallial gonoduct was correctly depicted in *Hua* by Prozorova (1990).

Dazo (1965), as well as several other workers (Woodard, 1934; Jones and Branson, 1964), have

Table 2. Summary of morphological differences between *Pleurocera acuta* and *Elimia livescens* compared to other limnic gastropods classified in the Pleuroceridae and Melanopsidae. Details from Itagaki, 1960; Bilgin, 1973; Houbrick, 1988; Nakano and Nishiwaki, 1989; Glaubrecht, 1996; Strong and Glaubrecht, unpubl. data.

	Pleuraceura acuta *Elimia livescens*	*Juga*	*Semisulcospira*	*Melanopsidae*
External Anatomy:				
Ovipositor pore	Simple, weakly glandular	Simple, weakly glandular	Not applicable	Complex, highly glandular
Alimentary System:				
Salivary glands	Tubular	?	Tubular	Tubular/branched
Salivary gland position	Pass through nerve ring	?	Pass through nerve ring	Pass through/anterior to nerve ring
Esophageal gland	Absent	?	Absent?	Present
Digestive gland ducts	2	?	2	1
Caecum	Small	?	Small	Deep and spiral
Reno-Pericardial System:				
Bladder	Small, pallial	?	?	Small, pallial
Nervous System:				
Dialyneury, Zygoneury	Zygoneury	?	Dialyneury?	Zygoneury
Reproductive System:				
Seminal vesicle	Straight	?	Straight	Coiled
Pallial oviduct	Open	Open	Closed	Open
Seminal receptacle	Absent	Present	Present	Present
Reproductive strategy	Oviparous	Oviparous	Viviparous	Oviparous

reported the presence of a seminal receptacle, but no mention of a spermatophore bursa was made. The present study has confirmed that the sperm storage structure in *Pleurocera acuta* and *Elimia livescens* is a bursa based on the presence of unorientated sperm. Examination of specimens of *E. laqueata* (USNM 1081558) confirmed that the structure reported as a seminal receptacle is indeed a bursa—no seminal receptacle is present; judging from the description of Jones and Branson (1964), the same holds true for *E. potosiensis*. The pallial position of the bladder was also confirmed in *E. laqueata* (pers. obs.). It is interesting to note that the sperm gutter extends farther anteriorly in *E. laqueata* than in *E. livescens*. Additionally, the straight segment of the albumen gland between the tip of the bursa and the junction of the renal oviduct is lacking in *E. laqueata*. Instead, the albumen gland arcs dorsally to join the renal oviduct just behind the tip of the bursa. In all other respects, the overall structure of the pallial oviduct in *E. laqueata* is consistent with features described here, as well as in the close association between the ovipositor and the junction of the propodium and mesopodium.

A final discrepancy is the presumed site of spermatophore formation. Woodard (1934, 1935) described the distal prostate as smooth and the highly folded proximal portion as the site of spermatophore formation. Jones and Branson (1964) did not distinguish a spermatophore-forming region in *Elimia potosiensis*. In the present study, it is the highly folded distal region that is inferred to be the site of spermatophore formation.

Systematics of Pleuroceridae

As mentioned above, although confusion has long existed, the distinctiveness of the Pachychilidae from other limnic lineages including the Pleuroceridae has now been clarified based on morphological and molecular data (e.g. Glaubrecht, 1996, 1999; Lydeard et al., 2002; Köhler et al., 2004). However, the paraphyly of eastern and western North American and Asian pleurocerids with respect to the Melanopsidae based on molecular data (Lydeard et al., 2002) remains at issue. The analysis of Houbrick (1988) did not include sufficient taxon sampling to adequately assess monophyly of the two families, but a sister-group relationship between the two was supported.

Although an in depth analysis of monophyly and affinity of the two families is beyond the scope of this study, several morphological features may be informative in clarifying these relationships. As noted by Prozorova (1990) the reproductive anatomy of eastern North American pleurocerids differs from species in western North America (*Juga*) and Asia (*Semisulcospira*) in that both *Juga* and *Semisulcospira* possess a seminal receptacle in addition to a spermatophore bursa. The latter genus has modified the pallial oviduct into a closed brood pouch (Itagaki, 1960; Nakano and Nishiwaki, 1989; Prozorova, 1990; Rashchepkina, 2000; Prozorova and Raschepkina, 2001, 2004).

In addition to the synapomorphies recovered in the analysis of Houbrick (weakly developed hypobranchial gland, zygoneury, long left pleural/sub-esophageal con-

nective), midgut anatomy is broadly congruent in the two families, differing in several significant respects from that of the other limnic lineages (e.g. Paludomidae, Pachychilidae, Thiaridae) (Bilgin, 1973; Köhler and Glaubrecht, 2001; Strong and Glaubrecht, 2002, 2003, unpubl. data). They also share similarities in reno-pericardial (presence of a bladder) and reproductive anatomy (open pallial gonoducts, presence of a seminal receptacle)—the latter, in particular, are undoubtedly symplesiomorphic. But other aspects of the anatomy are consistent within each family and clearly differentiate the two when sufficient information is available. Thus, in addition to features of the radula and shell, melanopsids may be distinguished by the presence of an esophageal gland, salivary glands that lie anterior to the nerve ring (although variable in the family), a single digestive gland duct and spiral caecum in the midgut, and a coiled seminal vesicle. Of course, the extent to which these features represent shared derived or homoplastic features remains to be discovered in the context of a phylogenetic analysis.

CONCLUSIONS

The present study has provided the first detailed description of the midgut and kidney for any pleurocerid snail, and has clarified the internal structure and homologies of the pallial gonoducts of eastern North American forms. This comparative analysis has confirmed the high degree of morphological similarity between *Pleurocera acuta* and *Elimia livescens*, but has also revealed a number of differences in detail; the extent to which these features support monophyly of the genera remains to be established. The fact that the presence/absence of a seminal receptacle distinguishes eastern and western North American/Asian pleurocerids is confirmed. Pleurocerids and melanopsids are broadly similar in features of the midgut and share a similar configuration of the pallial oviduct, but can be distinguished by anatomical characters of the alimentary (salivary glands, esophageal gland, digestive gland ducts, caecum) and reproductive (seminal vesicle) systems. However, comprehensive anatomical treatments of western North American and Asian pleurocerids are needed to fully assess the morphological distinctiveness of the two families. The clarification of the distribution of these features, within the context of a phylogenetic analysis, should aid in refining the monophyly of the Pleuroceridae and their affinity to other freshwater lineages.

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New Late Cretaceous (Santonian and Campanian) gastropods from California and Baja California, Mexico

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ABSTRACT

Three new genera and six new species of shallow-marine Late Cretaceous gastropods are reported from various formations in California and from one formation in Baja California, Mexico. *Tegula jeanae* new species, of early Campanian age, is the earliest known species of this trochid genus. *Nerita* (subgenus?) *orovillensis* new species is the second known Early Campanian neritid from California. The cerithioid *Bullamirifica* new genus is represented by three species: *Bullamirifica verruca* new species of Coniacian age; *Bullamirifica elegans* new species of early Campanian age; and *Bullamirifica ainiktos* (Dailey and Popenoe, 1966) of middle to late Campanian age. The latter species has the most widespread distribution, with occurrences in southern California and northern Baja California. *Minytropis melilota* new genus and species of Santonian age, and *Paxitropis dicriota* new genus and species of Late Santonian to early Campanian age are high-spired trichotropids. As presently known, *Bullamirifica*, *Minytropis*, and *Paxitropis* were endemic to the study area.

INTRODUCTION

This study is based largely on specimens collected by Eric Göhre of Oroville, California. Over the years, he has amassed a sizeable collection of shallow-marine mollusks from the lower Campanian Pentz Road member of the Chico Formation near Pentz, Butte County, northern California (Figure 1). His collection has yielded several new species of gastropods, and some of these were described by Groves (2004) and Squires and Saul (2004). In part, this present study concerns three additional new species and a new genus of gastropods found in his collection. They are the trochid *Tegula jeanae* new species, the neritid *Nerita* (subgenus?) *orovillensis* new species, and the cerithioid *Bullamirifica elegans* new genus and species.

Inspection of the literature, as well as examination of the collections at the Natural History Museum of Los Angeles County, allowed us to incorporate two additional species into *Bullamirifica*. These are *Bullamirifica verruca* new genus and species from the Coniacian Member IV of the Redding Formation in the Oak Run area, northern California, and *Bullamirifica anikitos* Dailey and Popenoe (1966) new combination from the middle Campanian Pigeon Point Formation southwest of San Francisco, northern California; the middle upper Campanian Punta Baja Formation, Baja California, Mexico; and the upper Campanian Jalama Formation, southern California (Figure 1). "*Cimolithium miyakoense*" (Nagao, 1934) and "*Vicarya* (*Shoshiroia*) *yabei*" Kamada, 1960, reported by Perrilliat-Montoya (1968) from Baja California, Mexico (see Figure 1, formation 6), are judged by us to be synonyms of *Bullamirifica ainiktos*.

Also included in this present study are new trichotropid gastropods found in the collections at the Natural History Museum of Los Angeles County. They are *Minytropis melilota* new genus and species from the Santonian part of the Redding and Chico formations of northern California, and *Paxitropis dicriota*, new genus and species from the of upper Santonian part of the Redding Formation, northern California; the lower Campanian part of the Chico Formation; and the lower Campanian part of the upper Holz Member of the Ladd Formation, southern California (Figure 1).

The geologic age of each new species described in this paper is shown in Figure 2. The entire interval of time that encompasses all these species is Coniacian to late Campanian, or about 19 million years. The new species are locally common, except for *Tegula jeanae*, *Nerita* (subgenus?) *orovillensis*, and *B. verruca*.

The classification system used here generally follows that of Hickman and McLean (1990) for the tegulines, Ponder (1988) for the trichotropids, and Ponder and Warén (1988) for the other taxa.

Study localities are listed in Appendix 1. Abbreviations used in the text are: CAS: California Academy of Sciences,

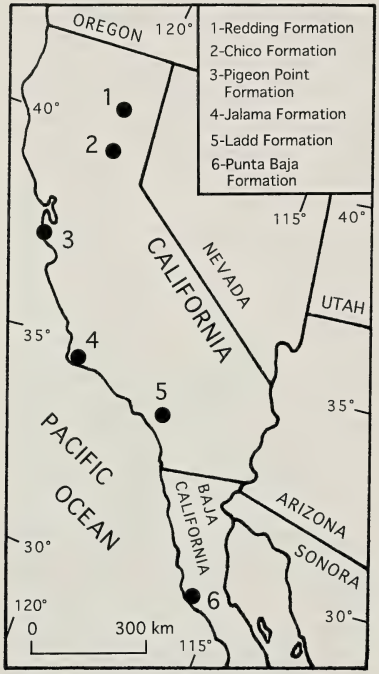


Figure 1. Location of formations bearing the new taxa.

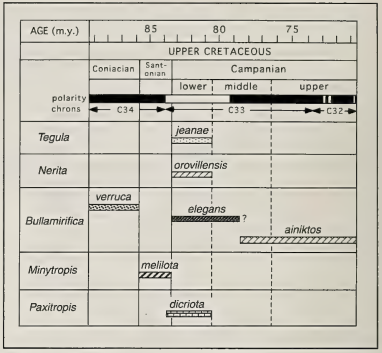


Figure 2. Chronostratigraphic positions of the new taxa. Ages of stage boundaries and magnetostratigraphy from Gradstein et al. (2004, fig. 19.1).

San Francisco; IGM: México Museo del Paleontologia del Instituto de Geologa; LACMIP: Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCLA: University of California, Los Angeles (collections now housed at LACMIP); UCMP: University of California Museum of Paleontology (Berkeley); USGS: United States Geological Survey.

STRATIGRAPHY

Except for the Punta Baja Formation, which is discussed below, the ages and depositional environments of all the formations and members containing the new taxa discussed in this paper can be found in the following papers: Member IV of the Redding Formation, Squires and Saul (2003a); Musty Buck Member of the Chico Formation, Saul and Squires (2003); Pentz Road member (informal) of the Chico Formation, Squires and Saul (1997); Ten Mile Member of the Chico Formation, Squires and Saul (2003b); upper Holz Shale of the Ladd Formation, Squires and Saul (2001); Pigeon Point Formation, Elder and Saul (1993) and Squires and Saul (2003b); and Jalama Formation, Squires and Saul (2003b). The locales of these formations are shown in Figure 1. Stratigraphic information mentioned below concerns additional pertinent biostratigraphic details. The age of the Jalama Formation used here is slightly younger than used in our previous papers because we had to adjust its chronostratigraphic position based on the latest published (Gradstein et al., 2004) absolute-time and global-paleomagnetic data correlations.

Punta Baja Formation

Perrilliat-Montoya (1968) reported specimens of gastropods, herein assigned to *Bullamirifica ainiktos*, from the "Rosario Formation" at Punta Baja, near El Rosario, northern Baja California, Mexico. The 5–140 m thick Punta Baja Formation (Figure 1) overlies fluvial deposits of the La Bocana Roja Formation, and the angular unconformity between these two formations is canyon-shaped (Boehlke and Abbott, 1986). This canyon is filled with conglomerate, sandstone, and siltstone reported by Kilmer (1963) to have been deposited in shallow-marine depths not exceeding 60 meters. Boehlke and Abbott (1986) have a differing viewpoint and reported that the deposits represent turbidites that accumulated in bathyal depths. They reported, furthermore, that shallow-marine mollusks are common, but Kilmer's collection at UCMP does not contain very many specimens. The Punta Baja Formation is unconformably overlain by terrestrial deposits of the La Escarpa Member of the El Gallo

Formation, which, in turn, is overlain by the Rosario Formation.

Based on molluscan fossils collected by F. H. Kilmer, Saul (1983: 21–22, fig. 9) reported the ammonite *Metaplacenticeras* cf. *pacificum* (Smith, 1900) and the gastropod *Turritella chicoensis pescaderoensis* Arnold, 1908, from the siltstone in the Punta Baja Formation. Although these two mollusks were reported by Saul (1983: 65–66) to be of late Campanian age, more recent biostratigraphic studies (Elder and Saul, 1996: fig. 1) depicted both of these taxa as ranging in age from late middle Campanian to earliest late Campanian. Adjustments for the most recently published (Gradstein et al., 2004) absolute-time and global-paleomagnetic data correlations place these ammonite and turritellid zones in the middle late Campanian. Recent examination by the junior author of additional Punta Baja Formation mollusks revealed three specimens of the bivalve *Calva*. The best preserved specimen is from LACMIP loc. 12582 and is *Calva* (*Egelicalva*) *crassa* Saul and Popenoe, 1992, whose geologic range is early late Campanian to early Maastrichtian elsewhere on the Pacific slope of North America (Saul and Popenoe, 1992). The other two *Calva* specimens are worn and broken, from UCMP loc. B-3388. These two specimens are similar to *Calva* (*Calva*) *peninsularis* (Anderson and Hanna, 1935), whose geologic range is latest Campanian to early Maastrichtian elsewhere on the Pacific slope of North America (Saul and Popenoe, 1992).

Boehlke and Abbott (1986: fig. 4) assigned the age of the Punta Baja Formation to the early Campanian based entirely on calcareous nannofossils. They also reported that the benthic foraminifera in this formation correspond to the F2-lower E foraminifera zones of Goudkoff (1945), but they did not rely on the foraminifera for their age call. Almgren (1986: table 2) reported that the F2-lower E foraminifera zones are essentially correlative to the early Campanian to late Campanian. It is important to mention that the Alcalde Shale in the Coalinga area along the west side of the San Joaquin Valley, central California, is correlative to the E zone (Almgren, 1986: table 3). As depicted in Saul (1983: fig. 10), the Alcalde Shale contains *Metaplacenticeras* cf. *M. pacificum*, and Almgren (1986) assigned the Alcalde Shale to the early late Campanian.

In summary, the *Metaplacenticeras*, *Turritella*, *Calva*, and benthic foraminifera data strongly support a middle late Campanian age for the Punta Baja Formation. The calcareous nannofossils, however, support an early Campanian age. It seems probable that the older calcareous nannofossils are reworked, and this would be consistent with the depositional environment of the formation.

SYSTEMATIC PALEONTOLOGY

Superfamily Trochoidea Rafinesque, 1815
Family Trochidae Rafinesque, 1815
Subfamily Tegulinae Kuroda, Habe and Oyama, 1971
Genus *Tegula* Lesson, 1835

Type Species: *Tegula elegans* Lesson, 1835, by monotypy; Recent, west coast of Central America to the Gulf of California, Mexico.

Discussion: Although Wenz (1938), Keen (1960), and Davies (1971) reported the geologic range of *Tegula* to be Miocene to Recent, Bandel and Stinnesbeck (2000) reported a species of *Tegula* of Late Cretaceous (Maastrichtian) age from central Chile. Kiel and Bandel (2001) reported a tentatively identified *Tegula* from upper Campanian strata in northern Spain. The early Campanian new species described below represents the confirmed earliest record we know of for *Tegula*. For the Pacific slope of North America, the previous earliest record of *Tegula* was given by Addicott (1973: 17, pl. 8, figs. 2, 4), who reported it from the Wygal Sandstone Member of the Temblor Formation, southwestern margin of the San Joaquin Valley, Kern County, central California. Squires (2003: table 2.1, fig. 2.1) placed this member in the lower Oligocene Matlockian Stage.

Tegula jeanae new species
(Figures 3–5)

Diagnosis: A *Tegula* with low to moderate spire. Whorls convex, smooth, and bearing one spiral groove on posterior third of last whorl. Anomphalous. Last whorl with raised lip along basal edge, base sunken between this lip and columellar lip, which bears at least one denticle and one much smaller denticle adapically.

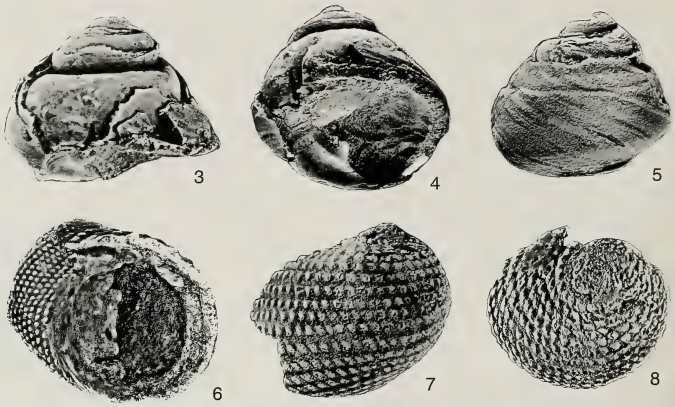
Description: Shell medium (up to 16.6 mm height and 21.7 mm diameter, same specimen). Turbiniform with spire low to moderately elevated. Protoconch unknown. Teleoconch consisting of three whorls. Suture impressed, slightly channeled. Whorls convex, sometimes slightly concave short distance anterior of suture; blunt angulation anterior of medial part of last whorl. Whorls smooth; spiral groove posterior of medial part of last whorl. Aperture oblique, peristome discontinuous. Anomphalous, umbilical area covered by broad callus. Base wide and smooth, peripheral (abaxial) margin coincident with raised lip along edge of last whorl; area depressed between this lip and columella. Outer lip strongly prosocline. Columellar lip with at least one oblique denticle; much weaker second denticle sometimes present immediately posterior of main denticle. Growth lines strongly prosocline, forming wide bands.

Holotype: LACMIP 13322, 18.7 mm in height, 22 mm in diameter.

Paratype: LACMIP 13323.

Type Locality: LACMIP loc. 24337.

Geologic Age: Early Campanian.



Figures 3–8. New tegulid and neritid gastropods. Specimens coated with ammonium chloride. **3–5.** *Tegula jeanae* new species, LACMIP loc. 24337. **3.** Paratype LACMIP 13323, apertural view, height 13.9 mm, diameter 17.9 mm. **4–5.** Holotype LACMIP 13322, height 18.7 mm, diameter 22 mm. **6–7.** *Nerita* (subgenus?) *orovillensis* new species. **6.** Holotype LACMIP 13324, apertural view, height 11.6 mm, diameter 16.8 mm. **7–8.** Paratype LACMIP 13325, total shell height 10 mm, diameter 13.7 mm. **7.** Abapertural view. **8.** Apical view.

Distribution: Chico Formation, Pentz Road member (informal), near Pentz, Butte County, northern California.

Etymology: Named for Jean Göhre, mother of Eric Göhre, who collected and donated the type material to LACMIP.

Discussion: This new species is known from two specimens, both showing good preservation. The new species is remarkably similar to *Tegula* (*Chlorostoma*) *funebralis* (Adams, 1855), from Pliocene and Pleistocene strata of southern California (Grant and Gale, 1931) and from the Recent of Vancouver Island, British Columbia, to central Baja California, Mexico (McLean, 1978). The new species differs from *T.* (*C.*) *funebralis* by having a smooth shell rather than being ornamented by weak spiral ribs. The similarity between the new species and *T.* (*C.*) *funebralis* is even stronger if the specimens of the latter are worn.

Tegula ovallei (Philippi, 1887: pl. 12, fig. 4; Bandel and Stinnesbeck, 2000: 761, pl. 1, B), the only other positively identified Cretaceous *Tegula* that we know of, is from Maastrichtian strata in central Chile. The new species differs from *T. ovallei* by having a smooth shell rather than being ornamented by granulated spiral ridges.

Kiel and Bandel (2001: 139, pl. 1, fig. 1) reported a tentatively identified *Tegula*? *simplex* (Quintero and Revilla, 1966: 49, pl. 8, fig. 3) from upper Campanian strata in northern Spain. The new species differs greatly from *T.*? *simplex* by having a less elevated spire, smooth shell, blunt rather than a sharp angulation anterior of the medial part of the last whorl, broad callus covering the umbilical region, wider aperture, very much stronger denticles on the columella, raised lip along the basal edge of the last whorl, and sunken base between this raised lip and the columellar lip.

Family Neritidae Rafinesque, 1815
Genus *Nerita* Linnaeus, 1758

Type Species: *Nerita peloronta* Linnaeus, 1758, by subsequent designation (Montfort, 1810); Recent, south Florida, West Indies, and Bermuda.

Discussion: *Nerita* sensu lato ranges from Early Cretaceous (Hauterivian), and the earliest record is from the Ono Member of the Budden Canyon Formation, Trinity County, northern California (Saul and Squires, 1997). The new species described below represents the first record of an early Campanian *Nerita* from the study area.

Subgenus?
Nerita (subgenus?) orovillensis new species
(Figures 6–8)

Diagnosis: A *Nerita* with approximately 18 to 19 beaded spiral ribs. Columellar lip with four or five obscure teeth.

Description: Shell medium small (up to 11.6 mm in height and 16.3 mm in diameter, same specimen), broader than high, globose. Last whorl rapidly expanding. Protoconch unknown. Teleoconch consisting of 2.5 to 2.75 whorls. Uppermost spire very low. Suture obscure. Earliest 1.5 teleoconch whorls apparently smooth, rest of teleoconch covered with approximately 18 narrow spiral ribs bearing small beads; interspaces between ribs approximately as wide as interspaces. Beads on ribs becoming smaller and slightly elongate on base of last whorl, especially in parietal region. Spiral rib adjacent to suture can be slightly stronger than other ribs. Aperture large, nearly circular. Outer lip flared, interior smooth. Columellar lip with five somewhat obscure teeth, most posterior tooth widest and longest. Deck area broad, sloping, and sharply demarcated from base of last whorl. Growth lines prosocline.

Holotype: LACMIP 13324, 11.6 mm in height, 16.8 mm in diameter.

Paratype: LACMIP 13325.

Type Locality: LACMIP loc. 24337.

Geologic Age: Early Campanian.

Distribution: Chico Formation, Pentz Road member (informal), near Pentz, Butte County, northern California.

Etymology: Named for Oroville, California.

Discussion: The new species is based on two specimens. The external surfaces are moderately well preserved, but the columellar lip and especially the deck area are poorly preserved.

The new species is remarkably similar to *Nerita* (*Theliostyla*) *crooki* Clark (1938: 700, pl. 4, figs. 1, 2) from the Markley Formation east of San Francisco, Solano County, northern California. Squires (2003: table 2.1, fig. 2.1) assigned this formation to the middle Eocene ("Tejon Stage"). The new species differs from *N.* (*T.*) *crooki* by having fewer and wider teeth on the columellar lip, fewer ribs on the last whorl with relatively wider interspaces, and ribs near the middle of the last whorl not noticeably broader than adjacent ribs.

The new species is also very similar to *Nerita umzambiensis* Woods (1906: 311, pl. 37, figs. 14–15; Bandel and Kiel, 2003: 51–52, pl. 1, figs. 4–5) from the Santonian/Campanian Umzamba Formation in southeastern South Africa. The new species differs from *N. umzambiensis* by having fewer teeth on the columella lip, ribs on the base of the last whorl, and a deck area sharply demarcated from the base of the last whorl.

The new species somewhat resembles *Nerita* (*Theliostyla?*) *kennedyi* Squires and Saul (2002: 185–187, figs. 31–34) from the upper lower to lower middle Eocene ("Domengine Stage") Santiago Formation, northern San Diego County, southern California. The new species differs from *N.* (*T.?*) *kennedyi* by having beads that are not elongate, wider interspaces between the ribs, and fewer, stronger, and wider teeth on the columellar lip.

The only other early Campanian neritid known from the Pacific slope of North America is *Neritina* (*Dostia*) *cuneata* (Gabb, 1864: 137, pl. 21, fig. 97) from lower Campanian strata at Tuscan Springs on Little Salt Creek, Tehama County, northern California. Gabb's species might also be present in 1) upper Campanian and/or lower Maastrichtian strata in the Pozo area, San Luis Obispo County (Vedder, 1977) and 2) Maastrichtian strata along the western edge of the San Joaquin Valley, California (Woods and Saul, 1986). The new species is vastly different from *Neritina* (*Dostia*) and does not have its patelliform shape nor its distinctive collabral sculpture.

Superfamily Cerithioidea Férussac, 1819
Family Indeterminate

Discussion: The new genus described below is most likely a cerithioid, on the basis of its sigmoidal growth lines, high spire, sculpture, short siphonal canal (slightly twisted), smooth columella, and smooth interior of the outer lip. Some specimens of the new genus have a narrow spire, like that found in cerithioids, but other specimens of the new genus have a buccinid-like shell. The strongly sigmoidal growth lines of the new genus, however, are unlike that found on buccinid shells. It is possible that the new genus belongs to a new cerithioid family.

Genus *Bullamirifica* new genus

Type Species: *Bullamirifica elegans*, new species; Early Campanian, Pentz area, Butte County, northern California.

Description: Shell medium (up to 83 mm height and 37 mm diameter, same specimen), fusiform to turreted. Height to diameter ratio 2 to 2.7. Spire high, comprising 41 to 55% of total shell height. Pleural angle 33 to 42°. Protoconch unknown. Teleoconch whorls six to eight. Spire whorls with shoulder angulate; last whorl with periphery angulate. Ramp short to moderately long, concave to rarely straight-sloped. Suture slightly undulatory, weakly impressed. Collabral sculpture consisting of many narrow ribs, closely to moderately widely spaced; interspaces smooth. Collabral ribs slightly opisthocline to opisthocyrt, usually extending from suture to suture. Collabral ribs present on base or obsolete; if present, swollen and elongate. Spiral sculpture consisting of several spiral ribs with variable width and spacing, especially on last whorl. Spire whorls with strongest spiral rib on whorl shoulder, several weak or moderately strong spiral ribs occasionally near anterior suture, and suture coincident with weak spiral rib either bearing weak nodes or without nodes. Last whorl sculpture with three to four widely spaced, strong spiral ribs on periphery and one or two weaker spiral ribs

or several spiral riblets on base. Intersections of collabral and spiral ribs producing many nodes or strongly projecting tubercles, either rounded (knob-like) to spinose or narrowly elongate. Nodes and knobs most pronounced on whorl shoulder, especially on last whorl. Intersections also strong on anterior portion of last whorl periphery. Aperture short but moderately wide, comma-shaped; small, narrow arch (canal-like) present where outer lip meets most posterior part of aperture. Columellar lip smooth. Siphonal canal short and spout-like or well developed, moderately short, and can be twisted to left. Outer lip thin, markedly sinuous, interior smooth. Growth lines sigmoidal between suture and shoulder; antispiral sinus coincident with tuberculate spiral rib.

Geologic Age: Coniacian to early late Campanian.

Etymology: Combination of the Latin *bulla*, meaning knob, and the Latin *mirifus*, meaning to cause wonder.

Discussion: Three species can be herein assigned to this new genus. Two of these species, *Bullamirifica verruca* and *Bullamirifica elegans*, are based on entirely new material. The third species was originally tentatively assigned by Dailey and Popenoe (1966) to *Pseudoglauconia* Douvillé, 1921. Dailey and Popenoe (1966) stated that this particular species belongs in a new genus, but they withheld their description until better specimens were obtained. Although representatives of the new genus have sigmoidal growth lines (see Wenz, 1940: 764, fig. 2214) similar to that of *Pseudoglauconia*, *Bullamirifica* differs considerably from *Pseudoglauconia* by having a bucciniform rather than a tapered/conical shape, angulate rather than flat-sided whorls, and tubercles on the sides of the whorls instead of only near the suture, and the suture between the penultimate and last whorl is not extremely deep and widely sunken. Unfortunately, the aperture of *Pseudoglauconia* is not known and none of the apertures on the available specimens of *Bullamirifica* is complete. In spite of the absence of knowledge about the aperture of *Pseudoglauconia*, Wenz (1940) believed this gastropod genus to belong in the Cerithiidae.

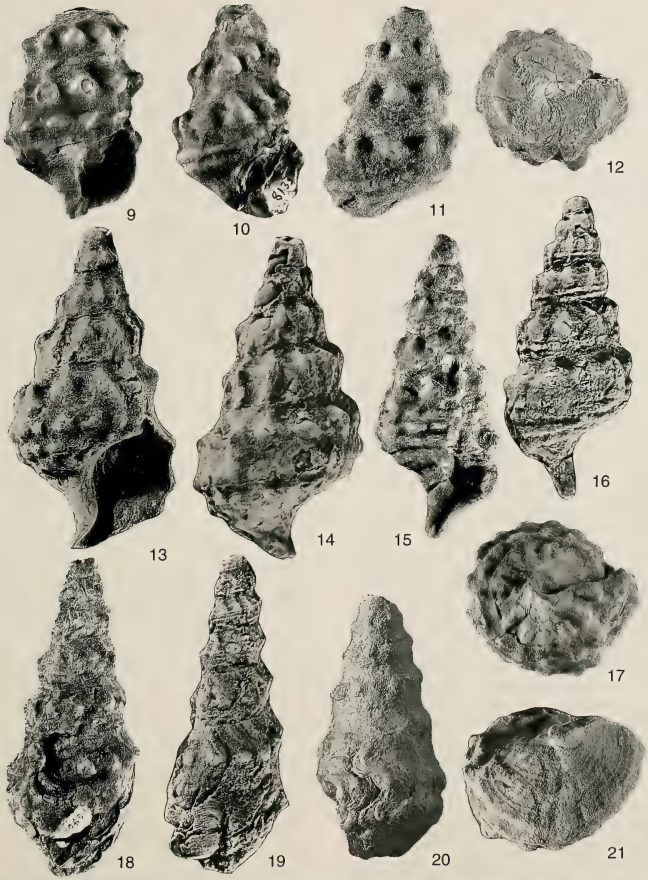
The shape of the growth lines in *Bullamirifica* is similar to that of *Batillaria echinoides clavatulata* (Lamarck, 1804) from the middle Eocene (Lutetian) of the Paris Basin, France. The siphonal canal of this Eocene species is longer than normally found in *Batillaria* Benson, 1842. Ponder and Warén (1988) and Houbrick (1988) placed *Batillaria* in superfamily Cerithioidea, family Batillariidae Thiele, 1929. The similarity in growth-line shape between *Bullamirifica* and *Batillaria* suggests to us that the new genus might be a cerithioid. The high turreted spire of *Batillaria*, however, is quite unlike the lower, more paucispiral spire of *Bullamirifica*.

Bullamirifica has the growth-line shape, shell shape, sculpture, and twisted siphonal canal similar to that of *Pseudorapa* Holzapfel, 1888, a monotypic genus from the Vaals Greensand in the Netherlands and Germany. The age of these strata was determined to be early Campanian by Albers (1976). Wenz (1941: 1083, fig. 3079) illustrated *Pseudorapa*. *Bullamirifica* differs from it by having a less twisted siphonal canal and more variable sculpture, including the possibilities of having spiral ribs and a relatively narrow shell. In addition, *Pseudorapa* has an outer lip that is very crenulate and a spiral band near the base of the last whorl that produces a tooth-like projection on the outer lip.

Bullamirifica verruca new species
(Figures 9–12)

Diagnosis: Small *Bullamirifica* with prominent rounded knobs, nine on shoulder of last whorl. Suture coincident with noded spiral rib. Base of last whorl without elongate collabral ridges. Siphonal canal short and straight.

Description: Small (up to 34 mm estimated height and 16.8 mm diameter, same specimen), fusiform, moderately slender. Height to diameter ratio approximately 2. Spire high, approximately 44% of shell height. Pleural angle approximately 35 to 37°. Protoconch and upper spire unknown. Teleoconch whorls approximately six (estimated). Spire whorls with shoulder angulate, last whorl with periphery angulate. Ramp short, concave. Suture slightly impressed, possibly undulatory. Collabral sculpture consisting of many ribs, widely spaced; interspaces smooth. Collabral ribs slightly opisthocline and extending from suture to suture. Collabral ribs mainly prevalent on ramp. Spiral sculpture consisting of several ribs with variable strength and spacing, especially on last whorl. Intersections of collabral and spiral ribs producing many strongly projecting rounded tuberculate knobs or, less commonly, nodes; knobs and nodes most prominent on shoulder and usually extending posteriorly across ramp and become narrow ridges. Spire whorls with strongest spiral rib on whorl shoulder, very faint spiral riblets present between whorl shoulder and anterior suture. Suture coincident with moderately weak spiral rib bearing small nodes. Penultimate whorl with spiral rib on shoulder bearing nine, moderately closely spaced knobs. Last whorl with three spiral ribs on periphery, strength of ribs progressively decreasing anteriorly: strong rib on shoulder and bearing nine very prominent tuberculate knobs; middle rib moderately strong and bearing more numerous nodes (about half sized of those on shoulder) that tend to become smaller and even obsolete adaxially; and most anterior periphery rib weakest and weak nodes tending to be obsolete adaxially. Base of last whorl usually with one or two spiral ribs, both bearing nodes (best developed near outer lip) or bearing no nodes, and with strength of spiral ribs decreasing anterior in direction; occasionally, anterior region of base with only very weak spiral riblets.



Figures 9–21. New cerithioid? gastropods. Specimens coated with ammonium chloride. **9–12.** *Bullamirifica verruca* new genus and species, LACMIP loc. 8133. **9.** Paratype LACMIP 13327, apertural view, height 27 mm, diameter 19.2 mm. **10–11.** Holotype LACMIP 13326, height 29.7 mm, diameter 17.8 mm. **10.** Apertural view. **11.** Abapertural view. **12.** Paratype LACMIP 13327, basal view, diameter 18.9 mm. **13–17.** *Bullamirifica elegans* new genus and species, LACMIP loc. 24337. **13–14.** Holotype LACMIP 13328, height 66.9 mm, diameter 34.9 mm. **13.** Apertural view. **14.** Abapertural view. **15–16.** Paratype LACMIP 13329, height 60.1mm, diameter 25.7 mm. **15.** Apertural view. **16.** Abapertural view. **17.** Holotype LACMIP 13328, basal view, diameter 35.7 mm. **18–21.** *Bullamirifica ainiktos* (Dailey and Popenoe, 1966) new genus. **18–19.** Hypotype LACMIP 13330, LACMIP loc. 10691, height 60 mm, diameter 24.1 mm. **18.** Apertural view. **19.** Abapertural view. **20.** Plasto-holotype LACMIP 40435, LACMIP loc. 24125, right-lateral view, height 58.2 mm, diameter 29.1 mm. **21.** Hyptotype LACMIP 13331, LACMIP loc. 24124, basal view, diameter 16.7 mm.

Aperture round with very small posterior "arch." Aperture elliptical, columellar lip smooth, outer lip thin; siphonal canal short and spout-like.

Holotype: LACMIP 13326, incomplete specimen with two whorls (upper spire missing), 29.7 mm height, 17.8 mm diameter.

Paratype: LACMIP 13327.

Type Locality: LACMIP loc. 8133.

Geologic Age: Coniacian.

Distribution: Redding Formation, Member IV, Oak Run area, northern California.

Etymology: Latin *verrucus*, wart.

Discussion: This new species is based on three specimens. It differs from *Bullamirifica elegans* new species below by smaller size and presence of rounded rather than elongate knobs, fewer knobs on shoulder of last whorl, no elongate collabral ridges on base of last whorl, a noded spiral rib coincident with the suture, and a straight siphonal canal. *Bullamirifica verruca* differs from *Bullamirifica ainiktos* by being smaller with a shorter spire and having rounded and much more projecting nodes, many fewer nodes on shoulder of last whorl, much less tendency for elongate collabral ridges on ramp, and much weaker spiral ribs between shoulder and anterior suture.

Bullamirifica verruca is very similar to the cerithioid *Tympanotonus* (*Tympanotonus*) *robustus* Dockery (1993: 47, pl. 7, fig. 1) in the shape of the spire, strong nodes on the spire, and shape of the growth lines next to the outer lip. *Tympanotonus* (*T.*) *robustus*, which is of Campanian age and from Mississippi, however, has no siphonal canal.

Bullamirifica elegans new species
(Figures 13–17)

[?] *Pseudoglauconia*? aff. *P. ainiktos* Dailey and Popenoe.—Elder and Saul, 1993: pl. 2, fig. 11.

Diagnosis: Large *Bullamirifica* with prominent opisthocline collabral ridges on upper spire and base of whorl. Shoulder of last whorl with 11 nodes. Suture coincident with unnoded weak spiral rib. Siphonal canal short but well developed and twisted to left.

Description: Medium large (up to 83 mm estimated height and 37 mm diameter, same specimen), fusiform, moderately wide, rarely slender. Height to diameter ratio approximately 2.2. Spire high, approximately 40% of shell height. Pleural angle approximately 33 to 42°, rarely approximately 30°. Protoconch and uppermost spire unknown. Teleoconch whorls approximately eight (estimated). Whorls with angulate shoulder. Ramp short and slightly concave. Collabral sculpture consisting of many moderately strong, narrow ribs; interspaces smooth. Collabral ribs extending from suture to suture. Collabral ribs sigmoidal between posterior suture and shoulder, opisthocline between shoulder and anterior suture. Collabral ribs somewhat swollen on base of last whorl. Spiral sculpture consisting of several ribs with variable strength and spacing. Intersections of collabral and spiral ribs producing many swollen, axially elongate nodes or, in some cases, rounded tuberculate knobs; nodes and knobs most prominent on shoulder. Spire whorls with strongest spiral rib on whorl shoulder and occasionally two moderately strong, noded spiral ribs between whorl shoulder and anterior suture. Suture coincident with weak spiral riblet. Penultimate whorl with spiral rib on shoulder bearing 11 widely spaced nodes. Last whorl with three or four spiral ribs on periphery, strongest rib on shoulder and bearing 11 nodes. Spiral ribs on periphery of last whorl usually show strength progressively decreasing anteriorly, occasionally rib immediately anterior of shoulder weaker than other ribs on periphery. Growth lines sigmoidal, with antispiral sinus coincident with shoulder. Aperture elliptical, columellar lip smooth, outer lip thin; siphonal canal short but well developed and slightly twisted to left.

Holotype: LACMIP 13328; nearly complete specimen of five whorls (upper spire missing), 66.9 mm height, 34.9 mm diameter.

Paratype: LACMIP 13329.

Type Locality: LACMIP loc. 24337.

Geologic Age: Early Campanian to possibly middle Campanian.

Distribution: Early Campanian: Chico Formation, Pentz Road member (informal), near Pentz, Butte County, northern California; Possibly middle Campanian: Pigeon Point Formation, San Mateo County, northern California.

Etymology: Latin *elegans*, meaning very fine or choice.

Discussion: The new species is based on six specimens from the Pentz area, and preservation is moderately good on all of them. Nearly all the specimens are moderately wide, but a few are somewhat slender, as the specimen illustrated in Figures 15–16.

There might be one specimen of the new species from the Pigeon Point Formation. This museum specimen, which cannot be located, was figured by Elder and Saul (1993: pl. 2, fig. 11). It was identified by them as *Pseudoglauconia*? sp. aff. *P. ainiktos* Dailey and Popenoe, but it has a profile somewhat more like *Bullamirifica elegans* and basal nodes like *B. elegans*. As will be discussed later, there are specimens of *B. ainiktos* from the Pigeon Point Formation. It seems likely that some of the *Bullamirifica* specimens from the Pigeon Point Formation represent transitional forms between *B. elegans* and *B. ainiktos*.

Bullamirifica elegans differs from *Bullamirifica verruca* in having larger size, prominent collabral ribs

extending from suture to suture on the spire whorls, swollen collabral ribs on the neck, more nodes on shoulder of the penultimate and last whorls, and siphonal canal longer and slightly twisted to the left. In addition, *B. elegans* occasionally has strong unnoded spiral ribs between suture and shoulder.

Bullamirifica elegans differs from *Bullamirifica ainiktos* by usually having a wider pleural angle, usually a less elevated spire, wider and stronger nodes on shoulder, fewer nodes on shoulder of last whorl, and base with swollen collabral ribs instead of fine spiral ribs. *Bullamirifica elegans* also has variability in morphology, whereas *B. ainiktos* does not.

Bullamirifica elegans is very similar to the cerithioid *Tympanotonus* (*Tympanotonus*) *binodosus* Dockery (1993: 47, pl. 7, fig. 2) in the shape of the spire, strong nodes on the spire, and shape of the growth lines next to the outer lip. *Tympanotonus* (*T.*) *binodosus* of Campanian age and from Mississippi, however, has no siphonal canal.

Bullamirifica ainiktos (Dailey and Popenoe, 1966) new combination
(Figures 18–25)

Pseudoglauconia? *ainiktos* Dailey and Popenoe, 1966: 21–22, pl. 6, figs. 3, 5, 6.
Pseudoglauconia? aff. *P. ainiktos* Dailey and Popenoe.— Elder and Saul, 1993: pl. 2, fig. 10.
Cimolithium miyakoense (Nagao, 1934). — Perrilliat-Montoya, 1968: 20, pl. 4, fig. 2.
Vicarya (*Shoshiroia*) *yabei* Kamada, 1960.— Perrilliat-Montoya, 1968: 21, pl. 6, fig. 1.

Diagnosis: Medium-size *Bullamirifica* with usually slender turreted whorls. Ramp on upper spire short, with narrow collabral ribs crossed by weaker spiral ribs; ramp on later whorls much longer and smooth and concave. Spire whorls concave on posterior half but angulate medially, with moderately strong tubercles. Shoulder of last whorl with 14 nodes. Base of last whorl with many, closely spaced spiral riblets. Siphonal canal short and possibly straight.

Description: Medium, up to 67.5 mm height estimated and 25.4 mm diameter, same specimen. Shell usually slender, turreted, occasionally wide, fusiform. Height to diameter ratio approximately 2.7. Spire high, approximately 55% of total shell height. Pleural angle approximately 33 to 37°. Protoconch unknown. Teleoconch whorls approximately eight (estimated). Spire whorls with shoulder angulate. Ramp usually short and concave, occasionally long and straight-sloped. Suture obscured. Collabral sculpture consisting of many spiral ribs closely spaced and narrow. Collabral ribs opisthocyrt, most prominent on ramp. Spiral sculpture consisting of several ribs, moderately weak and closely spaced. Intersections of collabral and spiral ribs producing many nodes, most prominent and somewhat spinose on shoulder. Spire whorls with strongest spiral rib on whorl shoulder and five moderately strong, non-noded spiral ribs between shoulder and anterior suture; most anterior one of these ribs coincident with suture. Penultimate and last whorls with approximately 14 nodes on shoulder. Last whorl with three spiral ribs on periphery, progressively weaker anteriorly, and bearing nodes. Base of last whorl bearing fine spiral riblets. Siphonal canal short and twisted to left. Columellar lip smooth. Outer lip sinuous; interior smooth.

Holotype: LACMIP 40435, incomplete specimen (tip of spire and siphonal canal missing), 39 mm height, 29 mm diameter.

Type Locality: LACMIP loc. 4125.

Geologic Age: Middle Campanian to Late Campanian.

Distribution: Middle Campanian: Pigeon Point Formation, near Pigeon Point, San Mateo County, northern California. Middle late Campanian: Punta Baja Formation, southwest of El Rosario, Baja California, Mexico. Late Campanian: Jalama Formation, Santa Barbara County, southern California.

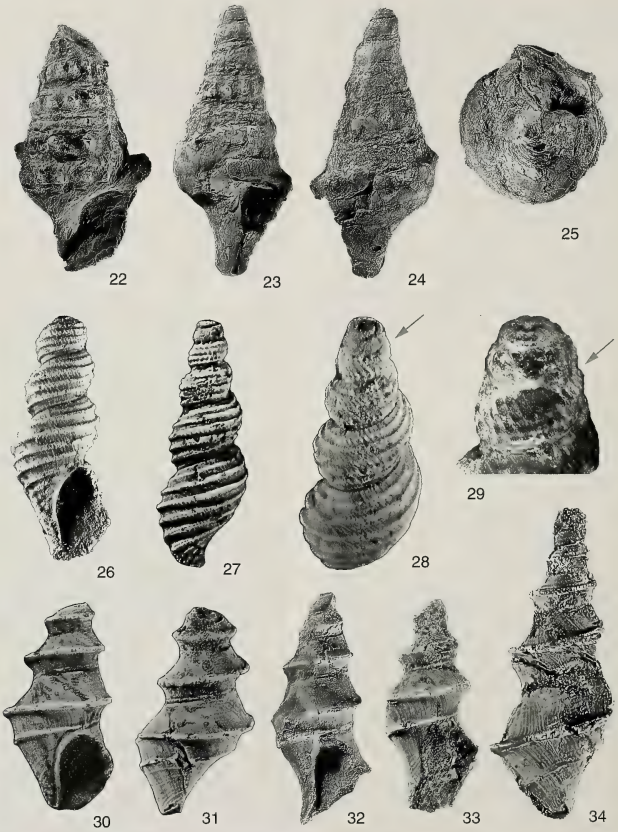
Discussion: Description of the new species is based on 25 specimens: 18 from the Jalama Formation, five from the Pigeon Point Formation, and two from the Punta Baja Formation. The Jalama specimens have poor to moderately good preservation, although the apices are broken off and the siphonal canal missing. The Pigeon Point specimens also have poor to moderately good preservation, but the matrix is very hard to remove. The Punta Baja specimens have poor preservation.

The Pigeon Point Formation specimen illustrated by Elder and Saul (1993: pl. 2, fig. 10) has a whorl profile like that found on *B. ainiktos* but it has wider pleural angle, similar to that found on *B. elegans*. Unfortunately this specimen is missing. As mentioned earlier, it seems likely that some of the *Bullamirifica* specimens from the Pigeon Point Formation represent transitional forms between *B. elegans* and *B. ainiktos*.

Bullamirifica ainiktos differs from *Bullamirifica verruca* by larger size and having less rounded and much lower nodes, more nodes on shoulder of last whorl, much more tendency for elongate collabral ridges on ramp, and much stronger spiral ribs between shoulder and anterior suture.

Bullamirifica ainiktos differs from *Bullamirifica elegans* by smaller size, having a narrower spire, usually a more elevated spire, narrower and weaker nodes on shoulder, more nodes on shoulder of last whorl, and base with fine ribs instead of swollen collabral ribs.

Perrilliat-Montoya (1968) identified one of the Punta Baja Formation specimens (Figures 23–25 herein) of *B. ainiktos* as *Vicarya* (*Shoshiroa*) *yabei* and identified the other specimen as *Cimolithium miyakoense*. With Wenz (1940: 740–741, fig. 2145) as a basis for comparison, we consider that *Bullamirifica ainiktos* differs considerably from the former gastropod by having a non-conical shell,



Figures 22–34. New cerithioid? and trichotropid gastropods. Specimens coated with ammonium chloride, unless otherwise noted. **22–25.** *Bullamirifica ainiktos* (Dailey and Popenoe, 1966) new genus. **22.** Hypotype LACMIP 13332, USGS loc. M-8601, height 35.8 mm, diameter 20 mm. **23–25.** Plasto-hypotype IGM 1325, height 80 mm, diameter 36.9 mm. **23.** Apertural view. **24.** Abapertural view. **25.** Basal view. **26–29.** *Minytropis melilota* new genus and species. **26.** Paratype LACMIP 13334, LACMIP loc. 10787, apertural view, height 7 mm, diameter 2 mm. **27–29.** Holotype LACMIP 13333, LACMIP loc. 10786, abapertural view, height 62 mm, diameter 2.2 mm. **27.** Abapertural view. **28.** Oblique apertural view of tip; arrow indicates where protoconch ends and teleoconch starts. **29.** Protoconch, height 0.5 mm, diameter 0.8 mm; arrow indicates where protoconch ends and teleoconch starts; SEM photomicrograph (uncoated). **30–34.** *Paxitropis dicriota* new genus and species. **30–31.** Paratype LACMIP 13336, LACMIP loc. 23643, height 12.7 mm, diameter 6.8 mm. **30.** Apertural view. **31.** Abapertural view. **32.** Holotype LACMIP 13335, LACMIP loc. 23639, apertural view, height 14.7 mm, diameter 6.6 mm. **33.** Paratype LACMIP 13337, LACMIP loc. 23642, apertural view, height 10.1 mm, diameter 4.4 mm. **34.** Paratype LACMIP 13338, LACMIP loc. 24217, abapertural view, height 11 mm, diameter 4.3 mm.

more rows of nodes, and absence of a notch on the outer lip near the suture and not having a thick, extensive callus that covers part of the noded sculpture near the suture on the last whorl. Using Kase (1984: 135–136, pl. 21, figs. 1–9; fig. 20) as a basis for comparison, we consider that *Bullamirifica ainiktos* differs considerably from the latter gastropod by having a much lower spire, more strongly sinuous growth lines, and a well developed, twisted siphonal canal.

Superfamily Capuloidea Fleming, 1822
Family Capulidae Fleming, 1822
?Subfamily Trichotropinae Gray, 1850

Discussion: We include a subfamily name because high-spired capulids, like those described below, are so distinctive from cap-shaped capulids. The subfamily allocation is tentative, pending much-needed taxonomic work on capulids.

Genus *Minytropis* new genus

Type Species: *Minytropis melilota* new species; Late Cretaceous, Santonian, northern California.

Description: Shell very small, estimated maximum height just over 10 mm. Shell thin, narrowly fusiform-elongate. Protoconch flat-topped and smooth, approximately two whorls. Teleoconch whorls rounded. Sculpture consisting of several strong spiral ribs with wide interspaces, both ribs and interspaces crossed by well delineated prosocline growth lines. Aperture oval, produced anteriorly to short, with narrow siphonal canal. Outer lip thin with no varix or inner denticulations. Inner lip callused, narrow.

Geologic Age: Early and Late Santonian.

Etymology: Combination of the Greek *minys*, meaning little, small, or short; and the Latin *tropis*, meaning keel.

Discussion: The placement of *Minytropis* among the trichotropids is suggested by the strongly prosocline and well marked growth lines, strong spiral sculpture, and the short, open siphonal canal. *Minytropis* resembles *Opposirius* Iredale, 1931, which is known only from the Recent of Australia (Wenz, 1940). *Minytropis* differs from *Opposirius* by having a narrower aperture, a longer siphonal canal, and a rounded rather than a bladelike inner lip.

Finlay and Marwick (1937) reported that *Opposirius* is more similar to *Cerithioderma* Conrad, 1860, than to any other trichotropid genus. In comparison to *Cerithioderma*, *Minytropis* is similar in having a flat-topped, smooth protoconch and in having a short siphonal canal, but *Minytropis* differs by having a much narrower shell, longer and much narrower aperture, stronger spiral sculpture, sculpture not recticulate on adult whorls, and no hint of an umbilicus. Wenz (1940) reported *Cerithioderma* to have a geologic range of Late Cretaceous to Oligocene, but Marwick (1965) reported that this genus is also extant. Dockery (1993) reported *Cerithioderma* from Campanian strata in Mississippi. High-spired trichotropids very similar to *Cerithioderma* are best represented in New Zealand Tertiary strata (Maxwell, 1992). According to Maxwell (1992), *Trichosirius* Finlay, 1926, might be a junior synonym of *Cerithioderma*.

Minytropis melilota new species
(Figures 26–29)

Description: Small, up to 10.2 mm estimated height and 3.5 mm diameter, same specimen. Shell narrowly fusiform-elongate. Spire high, 60% (estimated) of shell height. Pleural angle approximately 22°. Protoconch flat-topped, with two whorls, and smooth (0.5 mm height, 0.8 mm diameter). Teleoconch of approximately seven to eight subangulate whorls, last whorl nearly one-third total height. Suture deeply impressed, nearly coincident with very weak rib. Sculpture nearly cancellate on earliest teleoconch whorl, but four spiral riblets slightly stronger than numerous collabral threads. Sculpture on subsequent whorls progressing into five strong, flat-topped ribs on middle spire, six ribs on lower spire, and approximately eight to nine ribs on last whorl; most posterior spiral rib weak to very weak on all these whorls. Interspaces of nearly equal width on spire whorls but becoming twice as wide as ribs on last whorl. On last whorl, ribs on whorl face equally strong but on base, ribs become much less prominent and more closely spaced. Growth lines strongly prosocline, marked by fine collabral threads strongest on early whorls where they produce slight beading of spiral ribs. Growth lines less prominent and closer-spaced on later whorls; growth lines can be somewhat prominent on base of last whorl. Aperture oval, produced anteriorly to short, narrow siphonal canal. Outer lip thin, arcuate, crenulated by ribs. Columellar lip narrow, weakly callused, and barely forming a pseudo-umbilical chink between base of whorl and indistinct fasciole.

Dimensions of Holotype: Nearly complete specimen (siphonal canal mostly missing), 6.2 mm height, 2.2 mm diameter.

Holotype: LACMIP 13333.

Type Locality: LACMIP loc. 10786.

Paratype: LACMIP 13334.

Geologic Age: Early and Late Santonian.

Distribution: Lower Santonian: Redding Formation, Member V, Clover Creek, Shasta County, northern California. Upper Santonian: Chico Formation, Musty Buck Member, Chico Creek, Butte County, northern California.

Etymology: Latin *melitota*, meaning sweet clover (in reference to the occurrence of the new species near Clover Creek).

Discussion: Description of this new species is based on 29 specimens, most of which represented by small fragments. The better preserved specimens are all from the Redding Formation, however, none of these specimens is as large as the larger ones from the Chico Formation localities. Only two specimens, both from LACMIP loc. 10786, have retained the protoconch. The protoconch of one of these specimens is illustrated in Figures 27–29. The other specimen's protoconch is mostly embedded in hard matrix. The flat-topped protoconch of *M. meliota* supports the position of this gastropod among the Trichotropidae.

The new species can be distinguished from the similar looking *Opposirius idoneus* Iredale (1931: 210, pl. 22, fig. 7; Wenz, 1940: fig. 2631), an extant species in southwestern Australia, by having a narrower shell, one more rib on the spire, two to four more ribs on the base of the last whorl, a much longer siphonal canal, an a rounded columella. *Opposirius idoneus* is the type species of *Opposirius* Iredale, 1931.

Genus *Paxitropis* new genus

Type Species: *Paxitropis dicriota*; Late Cretaceous, late Santonian to early Campanian, northern California.

Description: Shell medium small, narrowly pagodiform. Spire whorls with prominent keel medially. Suture bordered posteriorly by relatively weak spiral rib becoming keel-like on last whorl and, in concert with aforementioned keel, producing bicarinate last whorl. Shell base with several weak spiral riblets. Growth lines prosocline. Columellar lip callused, abaxial margin well-delineated. Siphonal canal short but distinct. Anomphalous.

Geologic Age: Late Santonian to early Campanian.

Etymology: Combination of the Latin *pax*, meaning peace (in reference to the peaceful Pacific coast); and the Latin *tropis*, meaning keel.

Discussion: *Paxitropis* is similar to *Trichotropis* Broderip and Sowerby, 1829, a genus known (Sohl, 1960) from the Late Cretaceous to Recent. The modern distribution of *Trichotropis* is restricted to circum-boreal waters, in both the northern and southern oceans and, as Sohl (1960) noted, this modern distribution is in sharp contrast to its Cretaceous distribution in temperate shallow-water deposits. *Paxitropis* differs from *Trichotropis* by having a smaller size, much narrower shell (including a narrower aperture), a siphonal canal, much lower variability in sculpture, and being anomphalous.

Paxitropis resembles the trichotropid *Icuncula* Iredale, 1924, which is known from the Recent of the Indo-Pacific (Wenz, 1940). *Paxitropis* differs from *Icuncula* by having no hint of an umbilicus, less prominent keels that are unwavy, one less keel on the last whorl, and no axial riblets on the ramp. The aperture of *Paxitropis* is not entirely known.

The new genus has a whorl profile very similar to the turrid *Austrocarina* Laseron, 1954, known only from the Recent of New South Wales and Victoria, southeastern Australia and Tasmania. *Paxitropis*, however, is not a turrid because it does not have the turrid growth lines, which tend to be opisthocline anterior to the notch and across the whorl periphery curving toward prosocline very near the siphonal area.

Paxitropis dicriota new species
(Figures 30–34)

Description: Shell small, up to height estimated 14.5 mm and 6.6 mm diameter. Shell pagodiform. Spire high, approximately 60% of shell height. Pleural angle approximately 30°. Protoconch unknown. Teleoconch approximately six strongly angulated whorls, with wide ramp on middle spire whorls and on last whorl. Sculpture dominated by prominent spiral rib, medially located on shoulder and keel-forming on later whorls. Early teleoconch whorls with two spiral ribs anterior to carina. On mature whorls, these additional ribs become mere threads and equivalent in strength to growth lines, thus producing microscopic cancellate surface, especially on ramp. Suture impressed, nearly coincident with weakly noded subsutural spiral rib located immediately posterior to suture. Subsutural spiral rib relatively weak on spire whorls but becoming keel-like on last whorl. Last whorl with two sharp keels, one just above middle whorl height and second one weaker and occasionally minutely noded, emergent at anterior suture. Shell base with several weak spiral ribs. Growth lines prosocline, most prominent on shell base, near outer lip. Aperture lanceolate and produced anteriorly to short, but distinct siphonal canal. Outer lip thin, angulate, crenulated by ribs. Columellar lip callused, abaxial margin well-delineated. Columellar lip narrow, barely forming pseudo-umbilical chink between base of whorl and indistinct fasciole.

Holotype: LACMIP 13335, 14.7 mm height, 6.6 mm diameter.

Paratypes: LACMIP 13336, 13337, and 13338.

Type Locality: LACMIP loc. 23643.

Geologic Age: Late Santonian to Early Campanian.

Distribution: Upper Santonian: Redding Formation, Member VI, area east of Redding, Shasta County, northern California. Lower Campanian: Chico Formation, Ten Mile Member, Chico Creek, Butte County, northern California; Ladd Formation, upper Holz Shale Member, Santa Ana Mountains, Orange County, southern California.

Etymology: Combination of the Greek *di*, meaning two, and the Greek *criota*, meaning ringed.

Discussion: Twenty incomplete specimens were available, and the six most complete of these are the basis for the above description. The only specimen from the

Redding Formation is geologically the oldest specimen (LACMIP loc. 24217). The only specimen from the upper Holz Shale is from LACMIP loc. 21536.

The new species is very similar to the Pliocene to Recent *Trichotropis bicarinata* (Sowerby, 1825; Pitt and Pitt, 1989: pl. 1, figs. 3–4; Egorov and Alexeyev, 1998: 25, figs. 22–23), which is a Pacific upper boreal Arctic species, occurring in the waters off northern Japan, Kamchatka, southern Chukchi Sea, and Queen Charlotte Islands in British Columbia (Egorov and Alexeyev, 1998). The new species differs from *T. bicarinata* by having a much narrower last whorl and a much narrower aperture. These same differences distinguish the new species from *Trichotropis vokesae* Pitt and Pitt, 1989, which is extremely similar to *T. bicarinata*. *Trichotropis vokesae* is of Pliocene age and from northwestern Ecuador, and the new species differs from *T. vokesae* in the same ways that it differs from *T. bicarinata*.

The new species can be distinguished from the similar looking *Icuncula torcularis* (Tenison-Woods 1879; Wenz, 1940: fig. 2630), an extant species living off the coasts of southeastern Australia and Tasmania, by having less projecting and non-wavy keels, one less keel on the last whorl, and an absence of axial riblets on the ramp. *Icuncula torcularis* is the type species of *Icuncula* Iredale, 1924.

The new species is remarkably similar to the extant *Austrocarina recta* (Hedley, 1903; 1922: 223, fig. 3; Powell, 1966: 34, pl. 3, fig. 2; 1969: 364, pl. 276; Wilson, 1994: 187) but differs from *A. recta* by having a shell approximately 14 mm in height instead of 6 mm, a more projecting and usually wider keel on the shoulder of the adult whorls, several weak spiral ribs on base of last whorl, several spiral ribs on earliest teleoconch whorls, straight rather than a curved profile of the base, columellar lip callused with abaxial margin well-delineated, and no tendency to develop collabral ribs on earliest teleoconch whorls.

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APPENDIX 1

LOCALITIES CITED

Localities are LACMIP, unless otherwise noted. All quadrangle maps listed below are U. S. Geological Survey maps.

10786. Near crest of south slope of divide between Basin Hollow and Clover creeks, at approximately southeast corner of the northwest 1/4 of section 33, T. 32 N, R. 2 W. Lower Santonian. Redding Formation, Member V (lower part). Coll.: W. P. Popenoe and D. W. Scharf, August 8, 1931.

10787. Near crest of north slope of divide between Basin Hollow and Clover creeks, near northeast corner of northwest 1/4 of section 33 and not more than 122 m south of section line, T. 32 N, R. 2 W, Millville Quadrangle (15 minute, 1953), Shasta County, northern California. Lower Santonian. Redding Formation, Mem-

ber V (lower part). Coll.: W. P. Popenoe and D. W. Scharf, August 8, 1931.

12582. Turritellas and oysters along beach just south of La Bocana Roja Formation outcrop, approximately 2 km north of south tip on west side of Punta Baja, Mexico. Middle upper Campanian. Punta Baja Formation. Coll.: L. R. Saul, October 12, 1990.

21536. Corona Quadrangle, Santa Ana Mountains, Orange County, southern California. Lower Campanian. Ladd Formation, upper Holz Shale Member. Coll.: T. Bear, 1940.

23639. East bank of Chico Creek in concretions in massive, greenish-gray sandstone, 373 m south and 293 m west of northeast corner of section 23, T. 23 N, R. 2 E, Paradise Quadrangle (15 minute, 1953), Butte County, northern California. Lower Campanian. Chico Formation, Ten Mile Member. Coll.: L. R. and R. B. Saul, August 20, 1952.

23642. On W bank of Chico Creek, west of big westward projection of east lava cap and approximately N 27°W of BM 1770, 122 m south and 632 m west of northeast corner of section 26, T. 23 N, R. 2 E, Paradise Quadrangle (15 minute, 1953), Butte County, northern California. Lower Campanian. Chico Formation, Ten Mile Member. Coll.: L. R. and R. B. Saul, August 20, 1952.

23643. Concretionary sandstone on west side of Big Chico Creek, 670 m south and 762 m west of northeast corner of section 26, T. 23 N, R. 2 E, Paradise Quadrangle (7.5 minute, 1953), Butte County, northern California. Lower Campanian. Chico Formation, Ten Mile Member. Coll.: L. R. Saul and R. B. Saul, August, 1952.

24124. Hard, medium-grained, gray, arkosic sandstone, 158 m north of Jalama Creek, 3.3 km west and 0.6 km north of southeast corner of the topographic sheet, Lompoc Hills Quadrangle (7.5 minute, 1947). Upper Campanian. Jalama Formation. Coll.: D. Dailey and J. R. Dorrance, October, 1929.

24125. Hard, fine to medium-grained arkosic sandstone, 2.8 km west and 0.53 km north of southeast corner of the topographic sheet, Lompoc Hills Quadrangle (7.5 minute, 1947). Upper Campanian. Jalama Formation. Coll.: D. Dailey and J. R. Dorrance, October 29, 1929.

24217. Hard sandstone slabs in bed of Clover Creek, 213 m north and 366 m west of southeast corner of section 22, T. 32 N, R. 2 W, Millville Quadrangle (15 minute, 1953), Shasta County, northern California. Upper Santonian. Redding Formation, Member VI. Coll.: W. P. Popenoe and D. Dailey, August 27, 1959.

24337. Along east side of Highway 70, 792 m north and 305 m west of southeast corner of section 36, T. 21 N, R. 3 E, Cherokee Quadrangle (7.5 mintue, 1949), Butte County, northern California. Lower Campanian. Chico Formation, Pentz Road member (informal). Coll.: E. Göhre.

UCMP B-3388. In south-trending arroyo which reaches coast about 2.8 km north of the tip of Punta Baja. Marine invertebrates from massive, chert conglomerate at confluence of this arroyo and northwest-trending tributary about 122 m upstream from confluence. This locality is about 488 m northwest of the Punta Baja road. Middle upper Campanian. Punta Baja Formation. Coll.: F. H. Kilmer, date unknown.

USGS M-8601. In lens in sandstone on beach 0.5 km southeast of Bolsa Point, Pigeon Point Quadrangle, San Mateo County, northern California. Middle Campanian. Pigeon Point Formation. Coll.: W. P. Elder, 1989?

Daffymitra lindae, a new genus and species of Volutomitridae (Neogastropoda) from the Bellingshausen Abyssal Plain

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ABSTRACT

Daffymitra lindae, new genus, new species, is described from the Bellingshausen Abyssal Plain off Ellsworthland, Antarctica. Known only from its shell, this new taxon is included in the family Volutomitridae, but differentiated from all known living genera and species on the basis of its inflated shell shape, with an attenuated anterior and distinctive siphonal canal, as well as by the shape and disposition of its three recessed, obliquely oriented columellar plaits. This new taxon represents the first record of Volutomitridae from abyssal depths. The conchological similarity of *Daffymitra* to the Upper Cretaceous genus *Volutomorpha* raises the possibility that *Daffymitra* may be a surviving descendent of a lineage presumed extinct since the end of the Cretaceous, and suggests that a reassessment of the relationships between the various Cretaceous genera assigned to Volutoderminae and the earliest Volutomitridae.

INTRODUCTION

The Volutomitridae is a small family of rachiglossan neogastropods characterized by: a fusiform shell (reaching 50 mm) with 2–5 columellar plaits, and a paucispiral, mammilate protoconch; a radula with distinctive, wishbone-shaped rachidian teeth and small, needle-like lateral teeth that are present in most species; a mid-oesophagus that is long, convoluted, with a muscular posterior end; a gland of Leiblein that is only partially separated from the mid-oesophagus; and a single accessory salivary gland (Ponder, 1972, 1998; Kantor and Harasewych, 1992; Bouchet and Kantor, 2004). The family ranges into the North Pacific, North Atlantic and the Caribbean, but centers of diversity are concentrated in the southern hemisphere, particularly in the waters surrounding Antarctica, Australia, New Zealand, and especially New Caledonia (Bouchet and Kantor, 2004). Six genera and 50 species are currently recognized in the Recent fauna (Bouchet and Kantor, 2004), with a single genus (*Paradmete*) containing six species represented in the Antarctic and Magellanic fauna (Numanami, 1996; Bouchet and Kantor, 2004). Volutomitrids are known from the sublittoral zone to depths of 1980 m (based on dead specimens), but the majority of species are confined to outer continental shelf and upper continental slope depths (Bouchet and Kantor, 2004: Appendix; see Figure 7 herein).

In the course of our studies of Antarctic and sub-Antarctic neogastropods sampled by the United States Antarctic Program (USAP) and housed in the collections of the National Museum of Natural History (USNM), we encountered a single specimen of a volutomitrid that was collected on the Bellinghausen Abyssal Plain. This specimen represents a new genus and species within the family Volutomitridae, as well as the first record of the family from abyssal depths. This new genus and new species is described herein, and comparisons made with other volutomitrid taxa.

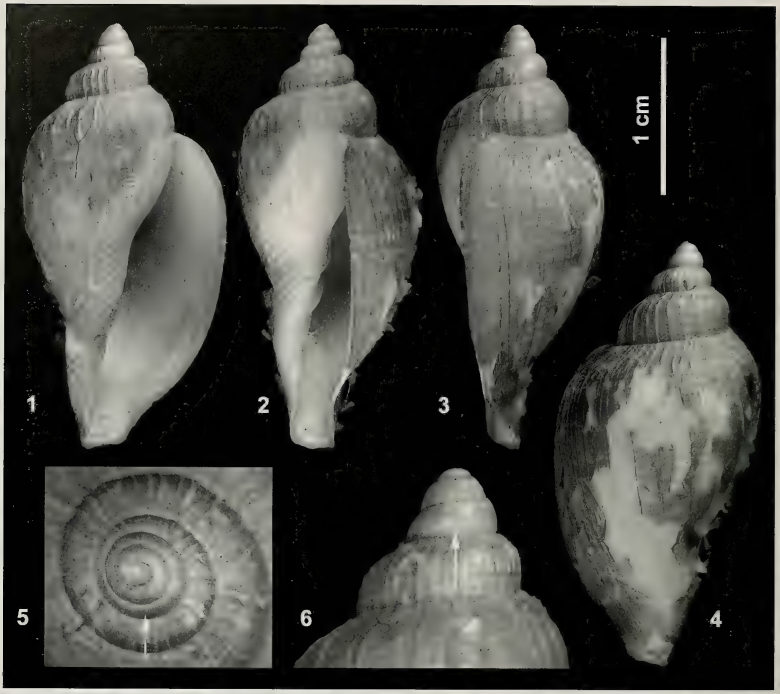
SYSTEMATICS

Class Gastropoda Cuvier, 1797
Order Neogastropoda Wenz, 1938
Family Volutomitridae Gray, 1854
Genus *Daffymitra* new genus

Type Species: *Daffymitra lindae* new species, by original designation.

Description: Shell medium-sized for the family (to 28 mm), with low, conical spire, broadly inflated body whorl. Protoconch conical, large, 2.6 mm in diameter, of 2 5/8 smooth whorls. Teleoconch thin, of about 3 smoothly rounded whorls, with well demarcated, broad siphonal canal. Axial sculpture of distinct, very narrow, broadly spaced ribs that extend from suture to siphonal canal. Spiral sculpture of narrow, cords, alternating in prominence. Aperture high (74% of shell length) broadly ovate. Outer lip thin, smooth. Columella with three columellar folds (central strongest) and siphonal fold. Shell white. Periostracum thin, olive brown. Operculum, anatomy, radula, unknown.

Etymology: This genus is named after Daffy, a tortoiseshell longhair cat that belongs to the senior author's wife Linda.



Figures 1–6. *Daffymitra lindae* new species, holotype. **1.** Apertural view of the shell. **2.** Oblique view, shell is rotated slightly to expose the columellar plaits. **3.** Lateral view of the shell. **4.** Dorsal view of the shell. **5.** Apical and **6.** lateral views of the protoconch. Transition to teleoconch is marked by arrow.

Daffymitra lindae new species
(Figures 1–7)

Description: Shell (Figures 1–4) of moderate size (to 27.9 mm), thin, fragile, with matte surface, inflated, fusiform, tapering anteriorly, with conical spire. Protoconch (Figures 5–6) large, mammilate, 1970 µm in height, diameter increasing from 676 µm to 2570 µm in 2 5/8 convex whorls. Protoconch-teleoconch transition distinct (Figures 5, 6, arrow), marked by onset of weak closely spaced prosocline ribs. Teleoconch of 3 1/8 strongly convex, ovate whorls with rounded shoulder. Suture impressed. Axial sculpture of thin, sharply demarcated, weakly prosocline raised ribs, 42 on last whorl, 34 on penultimate whorl. Ribs closely spaced on first teleoconch whorl, becoming more widely spaced on later whorls, but again closely spaced along final 1/8th whorl. Spiral sculpture of very low, narrow cords, subequal in width, alternating in prominence, covering entire shell surface, about 50 on final whorl, 10 on penultimate whorl. Aperture large (0.74 shell length), broadly oval, smooth, deflected from shell axis by 15°. Outer lip very thin, weakly reflected, edge forming final axial rib, with shallow anal sinus at suture. Columella weakly sinuate, convex posteriorly, distinctly concave medially, and again anterior to 3 obliquely oriented, recessed folds (Figure 2). Central fold most pronounced, anteriormost fold even more obliquely oriented than central and posterior fold. Parietal callus, broad, very thin. Siphonal canal broad, long, well delimited from

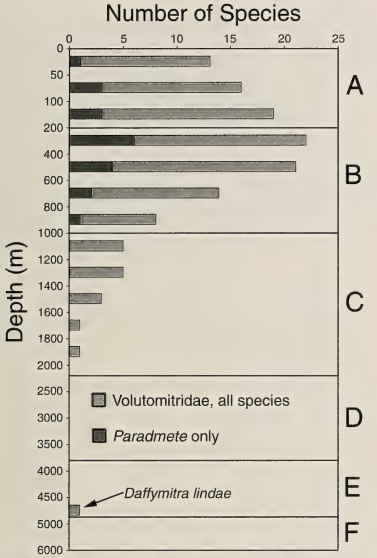


Figure 7. Bathymetric distribution of the Recent species of Volutomitridae, of the Antarctic genus *Paradmete* (data from Bouchet and Kantor, 2004: Appendix), and of *Daffymitra lindae*. A: continental shelf; B: upper continental slope; C: lower continental slope; D: continental rise; E: abyssal plain, F: hadal depths.

aperture. Shell color white. Periostracum thin, olive brown, covering entire shell. Operculum, radula and anatomy unknown.

Type Locality: Bellingshausen Abyssal Plain, 61°27′ S, 94°58′–95°22′ W, in 4419–4804 m [R/V ELTANIN cruise 23, sta. 1621, 10 Apr. 1966].

Type Material: Holotype, USNM 1080443, shell length 27.9 mm, final whorl length 23.4 mm, aperture length 21.5 mm, shell width, 13.5 mm.

Distribution: Known from the type locality only.

Etymology: This species is named for the senior author's wife, Linda Lee Harasewych.

Remarks: Despite the absence of anatomical and radular data, this new species can be unambiguously assigned to the family Volutomitridae on the basis of its distinctive shell shape, sculpture, presence of the diagnostic paucispiral mammilate protoconch, and weak columellar folds.

Seven genera are currently recognized within the family Volutomitridae (Cernohorsky, 1970; Bouchet and Kantor, 2004). The large size, long, broad aperture, and thin shell of this new species, as well as the presence of three obliquely oriented and deeply recessed columellar folds and a siphonal fold preclude its assignment to either the fossil genus *Proximitra* Finlay, 1927, or the Recent genera *Conomitra* Conrad, 1865; *Microvoluta* Angas, 1877; *Peculator* Iredale, 1924; or *Magdalemitra* Kilburn, 1974.

Conchologically, the new species is closer to the genera *Volutomitra* H. and A. Adams, 1853 and *Paradmete* Strebel, 1908, which are considered to be closely related (Powell, 1951: 165; Cernohorsky, 1970: 91). The 13 known species of *Volutomitra* are widely distributed in the World Ocean, ranging from South Africa, Southern Australia, New Zealand and to the Bering Sea in the Pacific, and from Colombia to the northern part of the Atlantic Ocean. *Daffymitra lindae* differs from all known species of *Volutomitra* in having a proportionally shorter spire and inflated rather than fusiform shell, coarse spiral sculpture and sharp, narrow, broadly spaced axial ribs, as well as columellar folds that are weak, recessed within the aperture and obliquely oriented rather than being strong, prominent, and nearly perpendicular to the columellar axis. The only species of *Volutomitra* with pronounced axial sculpture, *V. erebus* Bayer, 1971, from Colombia, has axial ribs that are thicker, more rounded, orthocline, and more densely spaced.

The genus *Paradmete*, contains six species, all confined to Antarctic and sub-Antarctic waters. *Daffymitra lindae* may easily be distinguished from *Paradmete fragillima* (Watson, 1882), the type species, as well as from *P. briedensis* Numanami, 1996, and *P. arnaudi* Numanami, 1996, by its larger size, shorter spire, inflated rather than narrowly fusiform shell, and distinctive narrow, prosocline axial ribs, as well as by its well demarcated siphonal canal. The Magellanic *Paradmete crymochara* (Rochebrune and Mabille, 1885) approaches *Daffymitra lindae* in size, but differs in its elongate, fusiform shape, absence of a distinct siphonal canal, and presence of four columellar folds. The distinctive *Paradmete percarinata* Powell, 1951, can be recognized by its prominent peripheral carina, sharply shouldered shell and pronounced columellar folds that are nearly perpendicular to the columellar axis. Most similar to *Daffymitra lindae* is *Paradmete curta* (Strebel, 1908), which reaches a similar size, has a low spire, and has axial ribs, which, however, are opisthocline rather than prosocline. *Daffymitra* differs in lacking a strong shoulder and in having an inflated shell shape with an attenuated anterior and distinctive siphonal canal.

The shell of *Daffymitra lindae* bears a surprising resemblance to some members of the Mesozoic genus *Volutomorpha*, particularly *V. mutabilis* Wade, 1926 (see Wade, 1926: pl. 37, fig. 10, pls. 40, figs. 6, 9; Sohl, 1964: pl. 39, figs. 1, 2, 6). *Volutomorpha* was restricted to the Upper Cretaceous faunas of the Gulf and Atlantic

coastal plains (for a review, see Sohl, 1964: 252–254), and was "the giant of Cretaceous gastropods" (Wade, 1926: 20) with shell lengths extrapolated to exceed 45 cm. Pilsbry and Olsson (1954: 19) included *Volutomorpha* in the Cretaceous subfamily Volutodermatinae, which they placed in the family Volutidae together with Volutomitrinae. More recently, Dzhalilov (1977: 93) proposed a new subfamily Volutomorphinae, also within Volutidae, while Bouchet et al. (2005: 255) considered Volutomorphinae a synonym of Volutodermatinae, which they transferred from Volutidae to the extinct family Pholidotomidae.

While *Daffymitra* is easily distinguished from *Volutomorpha* by its far smaller size, thinner shell, absence of thick axial ribs, and lack of a pronounced shoulder, this conchological similarity raises the intriguing possibility that *Daffymitra* is a "living fossil," a surviving descendent from a group presumed to have become extinct at the end of the Cretaceous. Further research is clearly required to reevaluate the relationships between the various Cretaceous genera assigned to Volutoderminae and the earliest Volutomitridae.

DISCUSSION

The family Volutomitridae has a broad geographic range, but has previously been known only from continental shelf and continental slope faunas, while the genus *Paradmete* has been reported only from shelf and upper slope depths (Figure 7). The greatest diversities for both the family and the genus occur at upper continental slope depths.

Although *Daffymitra lindae* is represented by a single empty shell, the fragility of the shell, the presence of periostracum, and the fact that it was collected below the aragonite compensation depth indicate that the specimen could not have been dead for long, and that the species inhabits the area in which this specimen was collected. Thus, this taxon represents the first record of Volutomitridae from abyssal depths. In a survey of Antarctic and Magellanic Buccinoidea, Harasewych and Kantor (2004) found that the abyssal buccinoidean fauna of the region has no genera in common with the sublittoral or bathyal faunas, but that credible sister taxa and likely origins for at least some of the abyssal genera occur on the adjacent continental slope. Based on shell morphologies, the genera *Volutomitra*, *Paradmete*, and *Daffymitra* appear to represent a lineage within Volutomitridae distinct from the predominantly austral genera *Proximitra*, *Conomitra*, *Microvoluta*, *Peculator*, and *Magdalemitra*. The genus *Paradmete*, a member of the upper slope fauna of Antarctica, is likely the sister taxon of the abyssal genus *Daffymitra*.

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Exilia alanbeui, a new species from the Neogene of central Chile: the first record of *Exilia* (Gastropoda: Ptychatractidae) from South America

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ABSTRACT

A new species of the ptychatractid genus *Exilia*, *E. alanbeui* new species, is described from late Neogene sediments of the Navidad Formation, central Chile. This new species represents the first record, fossil or Recent, of the genus *Exilia* from the South American continent. Given that Recent species of *Exilia* are restricted to bathyal depths, the presence of representatives of the genus in fine siltstones of the Navidad and Ranquil formations lend support to a previous interpretation of bathyal depths for these deposits.

INTRODUCTION

The genus *Exilia* Conrad, 1860, has been placed in the family Turbinellidae by Maxwell (1988) and in the subfamily Ptychatractinae within the Turbinellidae by Kantor et al. (2001). The subfamily Ptychatractinae was removed from the Turbinellidae and raised to family level by Riedel (2000), as was suggested previously by Kantor and Bouchet (1997). Riedel (2000) placed the Turbinellidae together with other columellar plaits-bearing groups in his suborder Volutina while the Ptychatractidae were placed in the suborder Muricina based mainly on radula type and absence of columellar plaits. The most recent classification is that presented by Bouchet and Rocroi (2005), placing Ptychatractidae within Pseudolivoidea. The genus *Exilia* has been revised by Bentson (1940) and more recently by Kantor et al. (2001). The latter authors synonymized nine nominal genera, i.e., *Mitraefusus* Bellardi, 1873, *Mesorhytis* Meek, 1876, *Surculina* Dall, 1908, *Phenacoptygma* Dall, 1918, *Palaeorhaphis* Stewart, 1927, *Zexilia* Finlay, 1926, *Graphidula* Stephenson, 1941, *Benthovoluta* Kuroda and Habe, 1950, and *Chathamidia* Dell, 1956, containing fossil and Recent species with *Exilia* and recognized a total of nine living species. Fossil species were not formally treated by them but a number of species were figured for comparison. Previously, the Recent species of the synonymized genus *Benthovoluta* had been reviewed by Cernohorsky (1973) and Harasewych (1987). Species of *Exilia* are known from the Late Cretaceous (Coniacian) onward and fossil species are known from all continents except Africa and South America, "probably a reflection of insufficient studies of Cretaceous and Tertiary mollusks in these regions" (Kantor et al., 2001, p. 92). Some Cretaceous through Miocene species come from shallow-water deposits while deep-water occurrences are known since the late Eocene (Kantor et al., 2001). Recent species of *Exilia* are restricted to bathyal depths at tropical latitudes and in the New Zealand region (Kantor et al., 2001).

Geology of the Fossil-bearing Localities

The Navidad Formation (Darwin, 1846) and its equivalents have recently been re-interpreted as late Miocene bathyal basin deposits containing displaced intertidal to outer shelf sediments (Finger et al., 2003; Nielsen et al., 2003). Several fossiliferous sites have been sampled for micro- and macrofossils. Of these, two localities from the Navidad Formation (Figure 1B) and two from the Ranquil Formation (Figure 1C) yielded specimens of *Exilia* described here.

Locality PPP (Figure 1B) is a grey deep-water siltstone that today forms the intertidal platform at Punta Perro. Based on planktonic foraminifera this locality has been dated as late Miocene (Tortonian) by Tsuchi et al. (1990) and Ibaraki (1992), while new dating by Finger et al. (2003) suggests an even younger age. The fauna is of an unusual composition for the Navidad Formation, containing otherwise unknown species of *Struthiochenopus* (Zinsmeister and Griffin, 1995) and *Xenophora* (Nielsen and DeVries, 2002). The specimens coming from Pupuya (Figure 1B) were collected by

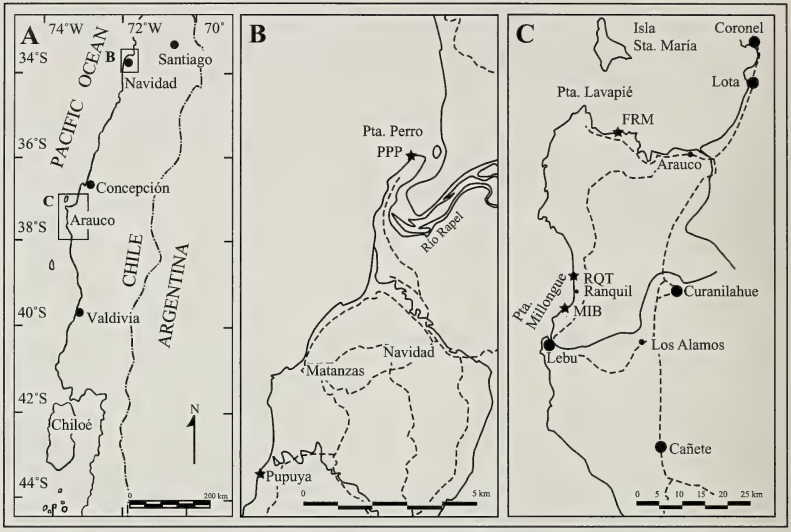


Figure 1. Fossil localities for *Exilia alanbeui* new species. in central Chile. **A.** Location of working areas. **B.** Localities of the Navidad Formation, Platform Punta Perro (PPP), Pupuya. **C.** Localities of the Ranquil Formation, Punta El Fraile (FRM), northern end of Caleta Ranquil (RQT), southwestern end of Caleta Ranquil.

V. Covacevich and D. Frassinetti a little south of the village Pupuya and come from a grey siltstone for which no ages are available. However, the faunal content (e.g., Nielsen et al., 2004) justifies correlation with PPP. The sediment at the type locality Punta El Fraile (FRM, Figure 1C) consists of grey siltstone and underlies a yellowish sandstone typical for the Ranquil Formation. The limit between these two lithological units has been observed to be a sharp, concordant one including some pebbles at the boundary. The sediments at Caleta Ranquil (RQT and MIB, Figure 1C) consist of a grey siltstone similar to that present at Punta El Fraile. The geological relation with other lithologies present at this locality, like reddish sandstone with beds of glauconitic sandstone and coarse light-grey sandstone, are not yet clear. However, both localities of the Ranquil Formation are similar to those of the Navidad Formation in lithology, and faunal content and were also dated as late Miocene by Finger et al. (2003).

MATERIALS AND METHODS

Specimens described in this study are deposited in the collections of the Departamento de Paleontología de Invertebrados Museo Nacional de Historia Natural, Santiago de Chile (SGO.PI) and Senckenberg Museum, Frankfurt, Germany (SMF). Photographs were taken using a Leicaflex SL2 or Olympus Camedia c730 camera. Images taken with the former camera were scanned from Ilford FP4 125 black and white 35 mm negatives using an Acer ScanWit 2720S film scanner. All images were processed with Adobe Photoshop 7.0.

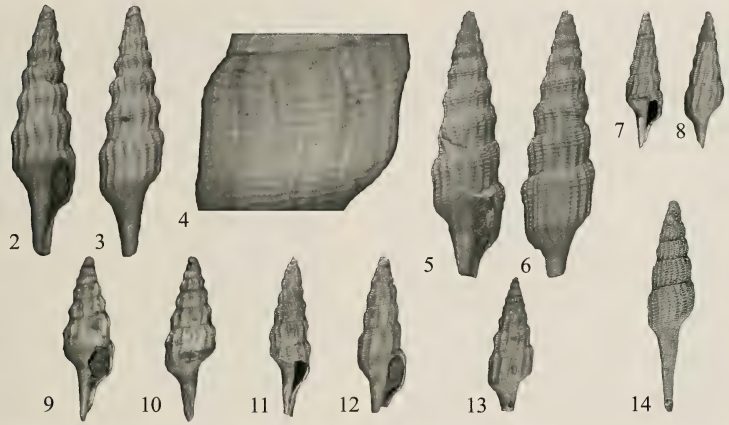
SYSTEMATIC PALEONTOLOGY

Family Ptychatractidae Stimpson, 1865
Genus *Exilia* Conrad, 1860

Type Species: *Exilia pergracilis* Conrad, 1860, by monotypy; Midway Group, lower Eocene, Alabama, USA.

Exilia alanbeui new species
(Figures 2–14)

Description: Shell narrow-fusiform, with spire occupying only little more than half of total height. Protoconch unknown. Teleoconch of about seven straight to slightly convex whorls, lacking pronounced shoulder. Axial sculpture consists of rounded, slightly



Figures 2–14. *Exilia alanbeui* new species. **2–4.** Holotype FRM 019 (height 28.35 mm). **5–6.** Paratype FRM 012-3 (height 30.2 mm). **7–8.** Paratype FRM 012-2 (height 15.46 mm). **9–10.** Paratype FRM 012-1 (height 9.3 mm). **11.** Paratype FRM 012-4 (height 18.03 mm). **12.** Paratype FRM 012-5 (height 17.62 mm). **13.** Paratype FRM 012-6 (height 15.2 mm). **14.** PPP 017 (PPP, height 23.9 mm).

backwards bent, collabral ribs. Penultimate whorl bears about 16 ribs, which become obsolete on base of whorl. Spiral sculpture well and equally defined, consisting of narrow, low, rounded, subequal cords, crossing axial elements unchanged, separated by interspaces of about equal width. Fine secondary spiral threads present in some interspaces. On penultimate whorl 10–14 spiral cords present, 8–9 further cords present on base of last whorl and about 30 weaker, closely spaced cords on siphonal canal. Aperture narrow-elongate. Outer lip thin. Siphonal canal narrow, long, straight. Inner lip smooth. Columella smooth and almost straight, with weak swelling at entrance of siphonal canal.

Etymology: This species is named in honour of Alan G. Beu (Institute of Geological and Nuclear Sciences, New Zealand), who always helps when needed.

Type Material: Holotype SGO.PI.6371 (FRM, height 28.35 mm), paratypes SGO.PI.6372 (FRM, one specimen, height 10.5 mm), SGO.PI.6373 (FRM, 21 specimens), SMF 327749 (FRM, 19 specimens).

Other Material Examined: SGO.PI.6374 (PPP, height 23.9 mm), SGO.PI.6375 (PPP, one specimen), SGO.PI.5303 (Pupuya, four specimens), SGO.PI.6376 (RQT, one specimen, height 9.25 mm), SGO.PI.6377 (MIB, one specimen, height 29.91 mm).

Type Locality: The grey siltstone at Punta El Fraile (FRM), Arauco, southern central Chile.

Occurrence: PPP, Pupuya, FRM, MIB, RQT; Navidad and Ranquil formations, Late Miocene or Early Pliocene, central Chile.

Discussion: *Exilia alanbeui* resembles the type species, *E. pergracilis* (see Bentson, 1940, pl. 2, fig. 25; Kantor et al., 2001, figs. 1 A–D), and *E. lincolnensis* Weaver, 1916, but differs from those North American Eocene species in having a less convex whorl profile, almost straight instead of sinusoidal axial sculpture and a more angulated whorl base. It differs from the New Zealand Miocene species *E. nodulifera* (Marwick, 1931), *E. leachi* (Marwick, 1931) and *E. wellmanni* Maxwell, 1988 (see Maxwell 1988) in having stronger axial sculpture. Most species of *Exilia* have more convex whorls and especially the Recent species have weaker axial sculpture (see Harasewych, 1987 and Kantor et al., 2001). The geographically closest species, *E. cortezi*, has wider whorls and different axial sculpture and is therefore not considered to be closely related to *E. alanbeui*. *Exilia alanbeui* is known only from localities consisting of deep water siltstones which have been dated as probably Messinian in age based on foraminifera (Finger et al., 2003). Therefore, this species is younger than the above mentioned Miocene species from New Zealand. Regarding the similarity of the two species, *E. alanbeui* may prove to be closely related to the New Zealand species *E. wellmanni*.

CONCLUSIONS

The occurrence of *Exilia alanbeui* in central Chile is the first record of the genus from the South American continent (except the Recent *E. cortezi* (Dall, 1908) from the Galápagos Islands) and therefore closes a considerable biogeographic gap. Although shallow water species of *Exilia* are known from Miocene deposits of Europe, the occurrence of *Exilia* in siltstones of the Navidad and Ranquil formations is here interpreted to support microfossil data placing these deposits in a bathyal environment (Finger et al., 2003).

Exilia alanbeui is another Chilean Miocene gastropod species that shows many similarities to New Zealand taxa. Trans-Pacific biogeographic connections between Chile and New Zealand during the Miocene have already been shown for some vetigastropods (Nielsen et al., 2004) and xenophorids (Nielsen and DeVries, 2002).

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Spawn of *Amphissa* sp. and *Cosmioconcha* sp. (Caenogastropoda: Columbellidae) from the Colombian Caribbean

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ABSTRACT

We describe the egg capsules and embryos of *Amphissa* sp. and *Cosmioconcha* sp. collected in the Caribbean Sea off Colombia between 20–160 m depth. *Amphissa* sp. had one layer of 24 egg capsules attached to the shell. *Cosmioconcha* sp. was completely covered by several layers of egg capsules; only the outer layer capsules contained embryos, the rest had the escape aperture open. Egg capsules of both species were translucent, dome-shaped, with an oval escape aperture at the center of the dome top. The surface was smooth, with no ridges nor sutures, and attached to the shell by an oval basal membrane that was surrounded by a thin, irregular flange. Egg capsules of *Amphissa* sp. measured 2 mm in diameter and contained 6 embryos/capsule at the gastrula stage; egg capsules of *Cosmioconcha* sp. measured 1 mm in diameter and contained 25 embryos/capsule at all stages of development (eggs, trochophores, and veliger larvae). Gastrulae of *Amphissa* sp. measured 750–900 µm in length and development in this species is probably direct. Uncleaved eggs of *Cosmioconcha* sp. measured 150 µm in diameter, the veliger had an operculum, a transparent shell measuring 188–219 µm in length, and a small velum; hatching occurs as planktonic larvae. No nurse eggs were observed in the two species but late cannibalism among sibling embryos may occur in *Cosmioconcha* sp.

INTRODUCTION

The family Columbellidae is very diverse in number of species in the Southern Caribbean. In this region, a total of 13 genera (*Columbella* Lamarck, 1799; *Rhombinella* Radwin, 1968; *Amphissa* H. and A. Adams, 1853; *Zafrona* Iredale, 1916; *Anachis* H. and A. Adams, 1853; *Nassarina* Dall, 1889; *Mitrella* Risso, 1826; *Cosmioconcha* Dall, 1913; *Aesopus* Gould, 1860; *Decipifus* Olsson and McGinty, 1958; *Mazatlania* Dall, 1900; *Strombina* Morch, 1852; *Nitidella* Swainson, 1840, and *Pyrene* Röding, 1798) and more than 30 species have been recorded (cf. Radwin, 1877 a, b; 1978; Costa, 2005); however, columbellid classification, as well as the identity and interpretation of the characters that support this classification, is not well resolved (DeMaintenon, 1999). The shells of these species are usually small and fusiform, within a size range of 5 to 24 mm and the outer lip usually bears denticles. The egg capsules and reproduction of several species have been described worldwide: Thorson (1940) summarized the different forms of egg capsules found in species from the Iranian Gulf, Knudsen (1950, 1995) described the egg capsules and development of species of tropical West Africa and the Azores, Amio (1957, 1963) described the eggs, larvae and embryology of Japanese species, DAsaro (1970) described the egg capsules of Panamanian Pacific species, Marcus and Marcus (1962) described the reproductive biology of several species from Brazil and Fortunato et al. (1998) characterized the reproduction of *Bifurcium bicanaliferum* (Sowerby, 1832) from the Pacific coast of Panama. In the Caribbean region, Bandel (1974) described the egg capsules of 10 species of Columbellidae from Santa Marta, Colombia; Penchaszadeh et al. (1983) characterized the reproduction of *Mazatlania consentini* Philippi, 1836 (as *M. aciculata*) (Lamarck, 1822) and Cipriani and Penchaszadeh (1993) that of *Strombina francesae* J. Gibson–Smith, 1974, and *Strombina pumilio* (Reeve, 1859), all three from Venezuela. Despite these studies, egg capsule morphology and developmental mode is still unknown for most of the recognized species.

Bandel (1974) distinguished 6 morphological groups of columbellid egg capsules according to the material he observed in Colombia and the literature. These are: (1) shallow domes on a broad, irregularly rounded disk of adhesion only extending on a narrow rim beyond the capsule walls as in *Mitrella ocellata* (Gmelin, 1791) reported as *Mitrella argus* (d'Orbigny, 1842), (2) cone shaped capsule, the walls rise from the round adhesion disk and end in a projecting edge forming a collar around the escape aperture, which is concave as in *Costoanachis sparsa* (Reeve, 1859), (3) cupola shaped with a suture dividing the capsule in 2 halves, oval base and the basal membrane extends in an irregular rim beyond the capsule walls, the escape aperture is asymmetrically located as in *Columbella mercatoria* (Linnaeus, 1758), (4) flask shaped and oval or round at the base, radial symmetry, the round adhesion disk is smooth and transparent, the capsule is sculptured with ridges as in *Nitidella nitida* (Lamarck, 1822), (5) brick

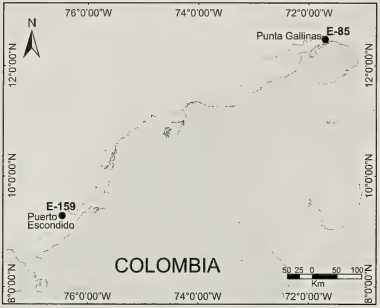


Figure 1. Map of the collecting localities in the Colombian Caribbean.

shaped egg capsules, escape aperture is absent as in *Anachis* sp. and (6) oval shaped standing on a peduncle as in *Columbella tryngas* Pils. A common spawning feature among these species was that they attached the egg capsules to hard substrates such as rocks, stems and algae (*Sargassum*), aquarium walls and hydroid stalks. Another spawning strategy found in the family involves attaching the egg capsules to the shells of conspecific living adults, such is the case of *Mazatlania consentini*, *Strombina pumilio*, *S. francesae* and *Bifurcium bicanaliferum* (Penchaszadeh et al., 1983; Cipriani and Penchaszadeh, 1993; Fortunato et al., 1998). There is no report in the literature for the Columbellid family of females using the shells of other living species as a substrate for egg laying.

In this paper, we describe the egg capsules and embryos of *Amphissa* sp. (*Amphissa* H. and Adams, 1853) and *Cosmioconcha* sp. (*Cosmioconcha* Dall, 1913) two apparently yet undescribed species from the Colombian Caribbean continental shelf. We also report on the number of egg capsules spawned by individual females and some reproductive parameters such as number and size of embryos contained in the egg capsules.

MATERIALS AND METHODS

One specimen of *Amphissa* sp. and three specimens of *Cosmioconcha* sp. were collected during 2001 by the Colombian ship B/I Ancon during an expedition to the Colombian Caribbean shelf (Figure 1). The specimen of *Amphissa* sp. was collected at Puerto Escondido, station E-159 at 158 m in muddy bottom (9°17′ N, 76°26′ W). The three specimens of *Cosmioconcha* sp. were collected at Punta Gallinas, station E-85 at 22 m depth in muddy-sand bottom (12°27′ N, 71°41′ W). Samples were obtained by trawling for 10 minutes with a trawling net type V measuring 12.7 m in total length and with a mesh size of 10 mm (Marinovich Trawl Co, Inc, USA). Samples were washed and separated in a 2 mm mesh seine, observed alive and preserved in ethanol 70%. The material of both species is deposited at the Museo de Historia Natural Marina de Colombia (MHNMC), INVEMAR, catalog numbers INV MOL3746 for *Amphissa* sp. and INV MOL5396 for *Cosmioconcha* sp.

The following reproductive aspects were studied: (1) number and size of egg capsules attached to each specimen, (2) number and size of embryos within each capsule and (3) observation of the different stages of development.

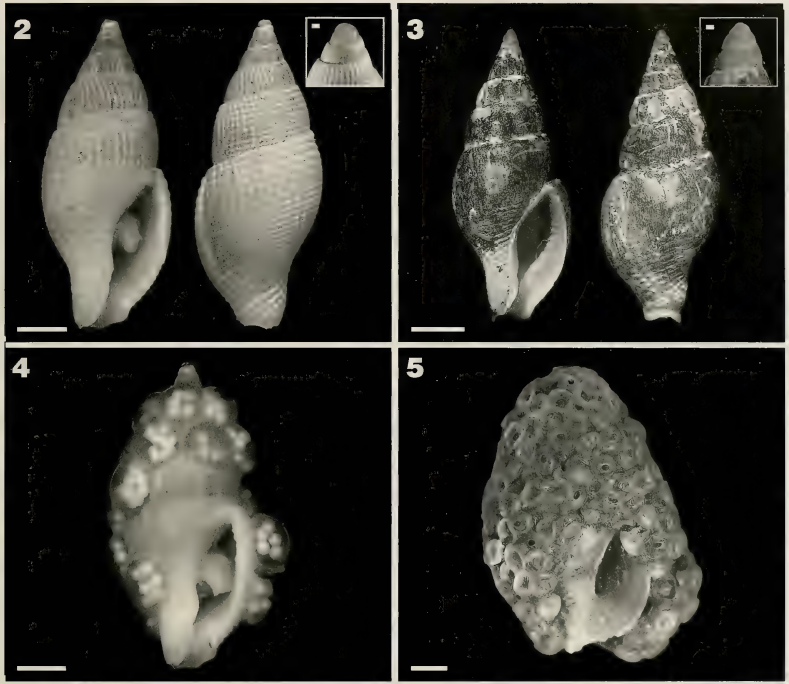
RESULTS

The specimen of *Amphissa* sp. (Figure 2) measured 12.5 mm and 5 mm in shell length and width respectively; the protoconch of this species measured 480 μm in length and had two whorls. A seemingly related species is *A. acuminata* (Smith, 1915) from the southern West Atlantic. Specimens of *Cosmioconcha* sp. (Figure 3) measured between 11 and 12 mm in shell length and between 4.5 and 5 mm in shell width; the protoconch measured 570 μm in length and had 3–3½ whorls. The taxonomic status of this species has to be confirmed.

A total of 24 egg capsules were attached to the shell of *Amphissa* sp. (Figure 4); these were arranged in one layer and covered most of the shell. The three specimens of *Cosmioconcha* sp. were completely covered by egg capsules in several layers that added 3 mm to the size of the shell (from 5 to 8 mm) (Figure 5). The egg capsules of the internal layers had no embryos and had their escape apertures open; the closed capsules containing embryos were limited to the external layer (Table 1).

The egg capsules of *Amphissa* sp. (Figure 6) were translucent, dome-shaped, with an oval escape aperture located on the center of the dome top. The capsule surface was smooth with no ridges nor sutures. They were attached to the shell by an oval basal membrane that was surrounded by a thin, irregular flange. Egg capsules measured around 2 mm in diameter and contained around 6 gastrulae embryos in each capsule. The egg capsules of *Cosmioconcha* sp. (Figure 7) were very similar to those of *Amphissa* sp. but smaller, measuring around 1 mm in diameter and containing around 25 embryos in each capsule at the three developmental stages examined: eggs, trochophore, and veliger larvae (Table 2). No nurse eggs were observed. The open egg capsules were filled with debris composed of organic matter and muddy sediment. Between the egg capsules, within the empty spaces, several specimens of the genus *Turbonilla* were found.

All egg capsules of *Amphissa* sp. contained embryos in the gastrulae stage in a number of six per capsule. The gastrulae were yellow, elongated, measuring 750–900 μm in length and 600–660 μm in width (Table 3). Each egg capsule of *Cosmioconcha* sp. contained embryos in the same stage of development; however, three different stages were identified in the spawn: uncleaved eggs, trochophore and veliger larvae (Table 3).



Figures 2–5. Shells and attached egg capsules. **2**. Adult shell of *Amphissa* sp. and detail of protoconch. Scale bar = 2 mm, detail = 200 µm. **3**. Adult shell of *Cosmioconcha* sp. and detail of protoconch. Scale bar = 2 mm, detail = 100 µm. **4**. Adult shell of *Amphissa* sp. covered by attached egg capsules. Scale bar = 2 mm. **5**. Adult shell of *Cosmioconcha* sp. covered by attached egg capsules. Scale bar = 2 mm. All photos taken from preserved material.

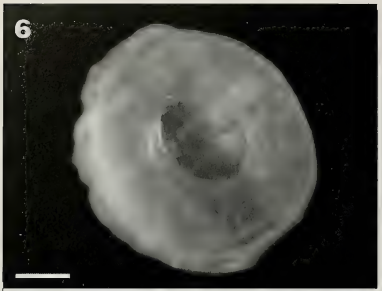
Table 1. *Cosmioconcha* sp. Number of layers and summary of the attached egg capsules for each of the three specimens collected (ND = not determined).

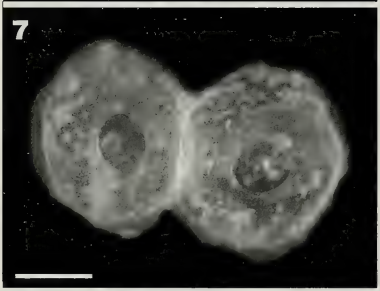
Specimen	1	2	3
Number of layers	4	6	4
Total number of attached capsules	537	775	494
Total number of capsules in external layer	ND	217	157
Number of open empty capsules	447	623	385
Number of closed empty capsules	3	0	1
Number of closed capsules containing embryos	86	152	108
Number of open capsules containing embryos	1	0	0

Empty embryonic shells were observed in a few capsules with embryos at the veliger stage. The uncleaved eggs measured 150 µm in diameter and the trochophore measured 165–212 µm in length. The veliger had an operculum and was characterized by a transparent, fragile shell measuring 188–219 µm in length and 156–194 µm in width. The velum was small, measuring 144–219 µm across from one lobe to the other and 31–94 µm in height; the cilia of this velum were very small, measuring 6–13 µm.

DISCUSSION

Amphissa sp. has not been previously reported in the Colombian Caribbean; the sediment at the locality





Figures 6–7. **6**. Egg capsule of *Amphissa* sp. Scale bar = 500 µm. **7**. Egg capsule of *Cosmioconcha* sp. Scale bar = 500 µm. All photos taken from preserved material.

where the specimen was collected is muddy, suggesting a broader habitat distribution for the species. The shell of this species resembles somewhat that of *A. acuminata* (Smith, 1915), a southwestern Atlantic species (Costa, 2005), but it is not as slender and the whorls are more rounded; the teleoconch consists of six rounded whorls and the sculpture of uniform spiral lirae and fine axial ribs, forming small rounded nodules at the intersections; aperture narrow, suboval; outer lip a little thickened exteriorly, with about five slender, short lirae within. For a detailed description of *A. acuminata*, see Simone and Leme (2001) and Costa (2005). The living species apparently most closely related to *Cosmioconcha* sp. is *Costoanachis helenae* Costa, 1983, whose distribution range is apparently restricted to the tropical sector of the Brazilian coast, from Amapá to Rio de Janeiro, in depths ranging from 8 to 100 m (Rios, 1994; Costa, 2005). We compared the egg capsules of *Cosmioconcha* sp. to those of *C. helenae* collected off Boipeba, an island on coast of the Brazilian state of Bahia (deposited at the Museu Nacional do Rio Janeiro, MNRJ 1029). The specimen measured 11.9 mm in length and 5.2 mm in width. Several spawning events had occurred on this shell since there were two layers of egg capsules, the external with about 30 and the internal with about 15 capsules, a number considerably lower than the number of capsules found in our species of *Cosmioconcha* (see Table 2). The capsules were very similar in shape to those of *Cosmioconcha* sp. but their size was larger; they measured 1.4 mm in length and 1.3 mm in width, and the aperture measured 0.6 mm in length and 0.5 mm in width (n= 10 capsules measured).

Cosmioconcha sp. was previously reported from the Colombian Caribbean as *Anachis* cf. *fraudans* Jung, 1969, a very closely related form from the Miocene-Pliocene of Trinidad (Díaz and Puyana, 1994). It also resembles *C. helenae* (Costa, 1983) in shell size and form, as well as in the number and form of embryonic whorls. However, the latter has a more slender spire, the upper half of its last whorl is sculptured with 11–18 axial ribs and its shell color is pale brown with white spiral bands (Costa, 2005). The last whorl of *Cosmioconcha* sp. lacks axial ribs and the shell is pale yellow under the dark brown periostracum. *Costoanachis helenae* has so far been only recorded from the central Brazilian coast, from Amapá to Rio de Janeiro (Rios, 1994; Costa, 2005).

The reproductive strategy of spawning or attaching the egg capsules to the adult shell of conspecifics is comparable to the spawning of other Caribbean species found in Venezuela, (Penchaszadeh et al., 1983; Cipriani and Penchaszadeh, 1993). However, it was not reported

Table 2. Summary of the egg capsule characteristics of *Amphissa* sp. and *Cosmioconcha* sp. Values represent mean ± SD, numbers in parenthesis indicate range (n = number of egg capsules measured).

Species Shell length (mm)	Capsule length (mm)	Capsule width (mm)	Capsule height (mm)	Aperture length (mm)	Aperture width (mm)	Embryos per capsule
Amphissa sp.	2.2±0.1	2.0±0.01	0.8±0.2	0.90±0.04	0.74±0.07	5.9±1.2 (4–8)
(12.5)	(2.0–2.4)	(1.9–2.1)	(0.6–1.0)	(0.78–0.93)	(0.60–0.90)	n=11
	n=18	n=18	n=18	n=11	n=11	(Gastrulae)
Cosmioconcha sp.	1.15±0.15	1.01±0.12	0.36±0.06	0.35±0.05	0.27±0.03	25.0±2.9 (19–31)
(11–12)	(0.75–1.5)	(0.75–1.47)	(0.24–0.50)	(0.27–0.54)	(0.02–0.02)	n=23
	n=63	n=63	n=62	n=62	n=62	(All stages)

Table 3. Size of embryos of *Amphissa* sp. and *Cosmioconcha* sp. during intracapsular development. Values represent mean ± SD and are reported in µm, numbers in parenthesis indicate range (n = number of embryos measured).

Species	Egg	Gastrula	Trochophore	Veliger	Protoconch (in adult)
Amphissa sp.	—	840±74 (750–900) n=6	—	—	500–600
Cosmioconcha sp.	150±0 n=16	—	189±19 (165–213) n=4	200±14 (188–219) n=7	570

for any of the 10 columbellid species studied by Bandel (1974) in the Santa Marta region, which attached the egg capsules to other hard substrates such as rocks, *Sargassum* plants, stalks of hydroids and, when in captivity, to the glass walls of the aquarium. There are no records in the literature of columbellids spawning on the shells of other species, a strategy that has been observed in the sandy beach gastropod *Olivancillaria deshayesiana* Ducros, 1857, from Argentina, which spawns the egg capsules on the adult shells of *Buccinanops monilifer* Kiener, 1834, and *Buccinanops duartei* Klappenbach, 1961, either directly on the adult shell or on top of the egg capsules of these species, which are also attached to the shell of conspecific individuals (Borzone, 1985). The fact that several layers of egg capsules are found, as well as different stages of embryonic development and empty egg capsules, on *Cosmioconcha* sp. suggests that several different events of oviposition have occurred using this specimen as substrate. Penchaszadeh et al. (1983) reported that females of *Mazatlania consentini* (as *M. aciculata*) attach their egg capsules to the shells of other individuals of the population with shells larger than 9 mm, apparently exclusively males, as shown by histological sections of the gonads of bearing individuals (Penchaszadeh, 1981). Fortunato et al. (1998) stated that the egg masses of *Bifurcium bicanaliferum* usually have several layers as well, whereas those of the Venezuelan Caribbean *Strombina pumilio*, *S. francesae*, and *M. consentini* have only one layer of egg capsules attached to the shell as we observed in *Amphissa* sp. Regarding this remarkable difference in the number of egg capsules that a single animal is bearing, we hypothesize that the egg capsules of species that bear few of them on the shell arranged on a single layer are easily detachable since they are usually individually attached, as is the case in *M. aciculata*. In this species, up to 20 egg capsules can be observed at the same time on one single adult shell; these have embryos at different stages of development, which means that not all egg capsules are spawned simultaneously. Once the veliger larvae hatch, the empty capsule usually falls off the shell, sometimes leaving only the basal membrane attached to the shell, and new capsules are spawned (Penchaszadeh, 1981). On the other hand, egg capsules of species with several layers are more resistant since they are attached not only to the adult shell by the basal membrane, but also form a very compact structure of egg capsules attached between them by lateral membranes (*B. bicanaliferum*, *Cosmioconcha* sp.). As pointed out by Pechenik (1986), gastropod egg capsules are structurally and chemically complex, the different layers are composed in general among and other components by protein and carbohydrates (Bayne, 1968; Miloslavich, 1996; Rawlings, 1999). Hunt (1966) also reported that since the capsule walls are extremely resistant to chemical treatment, the protein and carbohydrate components should be strongly linked in a glycoprotein complex and thus stabilized by sclerotization. In this way, the bond between two egg capsules is much stronger than the bond between an egg capsule and a shell.

The description of the egg capsule of *Amphissa* sp. is similar to the description provided by Bandel (1974) for *Zafrona pulchella* (cited as *Anachis pulchella*) in its dome shape. However, the dome of *Amphissa* sp. lacks the division into lower and upper parts separated from each other by one or a few concentric rings, it does not have a suture that continues the axis of the escape aperture and the membrane is not striped nor wrinkled. On the contrary, the surface is very smooth and only very thin imperceptible lines are visible. A comparable feature among both species is that the number of embryos per capsule was very similar and that no nurse eggs nor cannibalism seem to occur.

The egg capsules of *Cosmioconcha* sp. also fit in the first category of egg capsule morphology described by Bandel (1974), a simple dome attached by a rounded base. It is very similar to the capsule of *Amphissa* sp. but half its size in length, width and height. This capsule shape and general morphology are also comparable to the two species of the *Strombina* group from the Caribbean described by Cipriani and Penchaszadeh (1993), which have about the same size than the capsules of *Amphissa* sp., and to *B. canaliferum* from the Pacific coast of Panama described by Fortunato et al. (1998), which has about the same size than the capsule of *Cosmioconcha* sp.

No nurse eggs seem to be present in the two species studied. In comparison to other columbellid gastropods, the reproductive strategy of *Amphissa* sp. is similar to that of *S. francesae* and *S. pumilio*: large egg capsules (more than 2 mm in length), large eggs (more than 500 µm) and few embryos (about 4 to 8) that hatch as large crawling juveniles (larger than 0.9 mm). We did not observe the hatching stage of *Amphissa* sp., but the large size of the gastrula (about 840 µm) indicates that it

comes from a large egg which would most probably lead to direct development as in the two species of *Strombina* studied by Cipriani and Penchaszadeh (1993). On the other hand, the reproductive strategy of *Cosmioconcha* sp. is similar to that of *Bifurcium bicanaliferum*, *Anachis sparsa*, and *Cosmioconcha sertulariarum* (d'Orbigny, 1839): small egg capsules (about 1 mm in length), small eggs (about 140–200 µm) and many embryos (more than 20) that hatch as small veliger larvae (about 300 µm) (Fortunato et al., 1998; Marcus and Marcus, 1962). Late cannibalism among sibling embryos inferred from the presence of empty shells inside a few egg capsules of *Cosmioconcha* sp. has also been reported in *B. bicanaliferum* by Fortunato et al. (1998). Although late cannibalism might take place in the egg capsules of *Cosmioconcha* sp., it is very unlikely that this limited extraembryonic food source will allow the larva to grow from 200 µm to 600 µm, which is the protoconch size found in the adult shell. It is most likely that *Cosmioconcha* sp. will hatch as a veliger larva spending some time in the plankton as is also the case of *B. bicanaliferum*, which grows from 1.5 whorls to 2.5 whorls in the planktonic period (Fortunato et al., 1998). In the case of *Amphissa* sp., we can conclude from the size of its protoconch that this species must hatch as a crawling juvenile since the gastrula stage is already as large as the protoconch, a situation similar to what happens with the two *Strombina* species from the Venezuelan Caribbean studied by Cipriani and Penchaszadeh (1993).

We hope that in a near future, and thanks to the collection efforts carried out by INVEMAR in the southern Caribbean, more specimens will be collected. This will not only allow for the proper description of these species through use of traditional characters such as those from adult shell, anatomy, and radular morphology, but may also help increase the number of observations on egg capsules and the development of other embryonic stages.

ACKNOWLEDGMENTS

This work was partially supported by a Decanato de Investigación y Desarrollo, Universidad Simón Bolívar grant to the Grupo de Ciencias Marinas, by a FONACIT (S1-2001-000764) grant to the first author. Material collecting was possible through the "Macrofauna I and II" projects funded by COLCIENCIAS and INVEMAR. We are especially indebted to Paulo Márcio Costa, Departamento de Invertebrados, Malacologia, Museu Nacional, Rio de Janeiro, and Marta DeMaintenon, University of Hawaii at Hilo for helping with the problematic taxonomic status of our material. Paulo Marcio Costa also provided us with one reproductive specimen of *Costoananchis helenae* from Brazil for comparative purposes. We also wish to thank Pablo Penchaszadeh, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, for our fruitful discussions in the subject and José L. García Rondón, Artis Publishers, for his invaluable help with the photographs.

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Erratum

Due to an editorial lapse in the latest article by Cristián Ituarte (2005), please substitute the last sentence in the Etymology section (page 97, right-hand column, lines 24, 25) as follows:

Replace "..., which underwent a major cultural change during the past 10,000 years."

For: "..., which has been a major pathway for cultural exchange during the past 10,000 years."

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Ituarte, C. 2005. The Sphaeriidae (Bivalvia) from northwestern Argentina including three new species of *Pisidium*. The Nautilus 119: 93–104.

Pterorytis pacanana new species (Gastropoda: Muricidae): circumstantial evidence for late Pliocene El Niño events in southern Peru

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ABSTRACT

Pterorytis pacanana new species was discovered in upper Pliocene bioclastic sandstone near Chala, southern Peru. Although it was found farther south than other *Pterorytis* species from the eastern equatorial Pacific Ocean, *P. pacanana* most resembles *P. roxaneae* Petuch, 1994, from the Pliocene Pinecrest beds of Florida. Its presence among endemic late Pliocene cool-water mollusks from high-energy shoreface paleoenvironments is thermally anomalous in the same sense as the rare occurrence of other species from northern Peru and Ecuador in upper Pliocene and Pleistocene strata from southern Peru. By analogy with modern thermally anomalous mollusks that appear episodically off the coast of southern Peru and Chile, the Pliocene and Pleistocene examples are circumstantial evidence for the occasional southward incursion of warm equatorial waters during former El Niño events.

INTRODUCTION

Pliocene deposits in southern Peru are noted for a variety of muricid gastropods, most belonging to genera still represented by extant species (e.g., *Acanthina* Fischer von Waldheim, 1807; *Chorus* Gray, 1847; *Concholepas* Lamarck, 1801; *Crassilabrum* Jousseaume, 1880; *Muregina* Vermeij, 1998; *Stramonita* Schumacher, 1817; *Xanthochorus* Fischer, 1884), but some from genera entirely or locally extinct (e.g., *Herminespina* DeVries and Vermeij, 1997; *Trophon*, Montfort, 1810) (DeVries, 1995, 1997, 2000, 2003, in press a, in press b; DeVries and Vermeij, 1997). Specimens of most Pliocene muricids are not exceedingly difficult to find.

A well-preserved muricid from Pliocene bioclastic sandstone south of Chala is, literally, the rare exception. None have been found other than a single shell plucked from a roadcut of the Panamerican Highway that overlooks Playa Huacllaco. The lamellar fimbriate varices of the Huacllaco specimen invite comparison with ocenebrines from Ecuador, the southeastern United States, and the northwestern Pacific Ocean. Its lone appearance in a collection of endemic cool-water muricids is another example of a thermally anomalous molluscan species encountered in upper Pliocene and Pleistocene beds of southern Peru (Muizon and DeVries, 1985; DeVries, 1986; Ortlieb et al., 1990). A reasonable hypothesis is that these equatorial species were introduced to higher austral latitudes by warm-water incursions during the Pliocene and Pleistocene comparable to modern incursions that carry Panamic molluscan larvae poleward during El Niño events (DeVries, 1988; Arntz and Tarazona, 1990; Paredes et al., 1998).

Geology

Bioclastic sandstone and gravel and balanid coquina overlie igneous basement in roadcuts along a series of sweeping curves in the Panamerican Highway where it descends towards the beach at Playa Huacllaco (Figure 1). The sediments represent high-energy foreshore and intertidal paleoenvironments that once flanked steep cliffs. The section, previously published

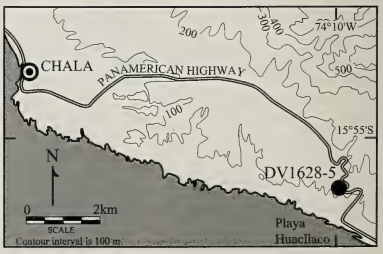

Figure 1. Type locality of *Pterorytis pacanana* new species (DV 1628).

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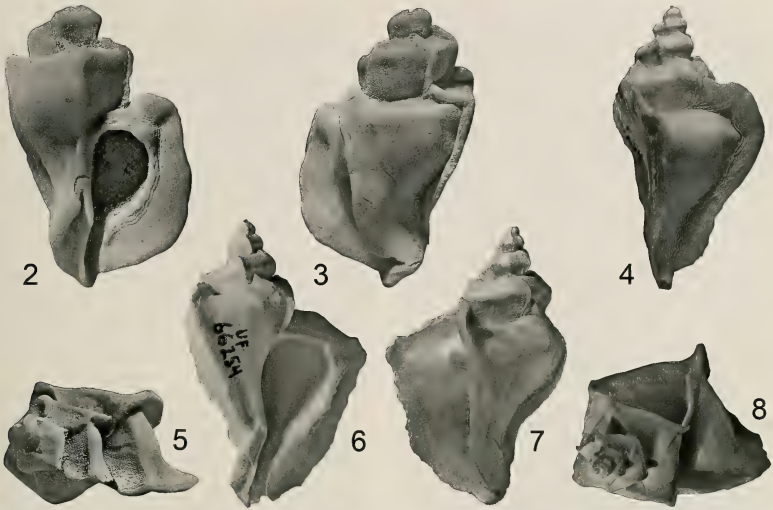

Figures 2–8. *Pterorytis* species. **2, 3, 5.** *Pterorytis pacanana* new species. Upper Pliocene. Holotype, UWBM 97772, length = 30.9 mm, width = 19.6 mm. **2.** Apertural view. **3.** Abapertural view. **5.** Oblique view of spire. **4, 6–8.** *Pterorytis roxaneae* Petuch, 1994. Upper Pliocene. Holotype, Florida Museum of Natural History, Gainesville, UF 66254, length = 33.3 mm, width = 21.5 mm. **4.** Lateral view. **6.** Apertural view. **7.** Abapertural view. **8.** Oblique view of spire.

by DeVries (2003), consists of four stratigraphic units. The ocenebrine specimen was found at the base of Unit III, just below strata where rounded clasts of blackened andesite first appear in great numbers and below beds where specimens of *Concholepas* and *Acanthina* acquire their modern form (DeVries, 2000, 2003).

The age of the Huacllaco beds is bracketed by basal beds with specimens of *Concholepas nodosa* Hupé, 1854, *Acanthina triangularis* DeVries, 2003, and *Herminespina mirabilis* (Möricke, 1896), which collectively indicate an early late Pliocene age (DeVries and Frassinetti, 2003), and the uppermost and oldest of several marine terraces, whose elevation and largely extant taxa suggest a latest Pliocene age (Muizon and DeVries, 1985).

MATERIALS AND METHODS

The specimen from Peru described in this study was found by the author. Dimensions affected by breakage are enclosed by parentheses. The holotype is deposited at the University of Washington's Burke Museum of Natural History and Culture in Seattle, Washington (UWBM).

SYSTEMATICS

Family Muricidae Rafinesque, 1815

Subfamily Ocenebrinae Cossmann, 1903

Genus *Pterorytis* Conrad, 1862

Subgenus *Pterorytis* sensu stricto

Type Species: *Murex umbrifer* Conrad, 1832, by monotypy.

Pterorytis pacanana new species
(Figures 2, 3, 5)

Diagnosis: Shell small; texture waxy, shell thin. Five lamellar, fimbriate varices; intervarical nodes absent. Three spiral cords; shoulder spiral cord strong. Sutural platform horizontal. Labral tooth absent.

Description: Shell 30.9 mm long (first teleoconch whorls missing), quadrate in profile, very thin, with waxy texture. Spire estimated to be about 40 percent of shell length. Siphonal canal about 20–25 percent of shell length. Protoconch and earliest teleoconch whorls missing. Upper sides of whorls planar, vertical; base of body whorl sharply constricted. Shoulder orthogonally

angulate, sutures deeply impressed; sutural platform horizontal to slightly concave. Three last whorls with five lamellar varices extending from fasciolar ridge to suture, each varix joining across suture with varix of previous whorl. Lamellae broader basally, narrower adapically, extended adapically at shoulder but not spinose; fimbriate on adapertural face; erect or recurved adaperturally except apertural lamellae, which is weakly recurved abaperturally. Intervarical nodes absent. Spiral sculpture of prominent but ill-defined rounded primary cord at shoulder angulation and two additional broad low spiral cords anteriorly, almost obsolete. Additional broad low secondary cords barely visible adjacent to adapertural face of varices. Lamellar fimbria slightly extended at intersection with primary spiral cords. Aperture with inverted tear-drop shape. Parietal rib, anal sulcus absent; parietal area unexcavated. Columella smooth, inner lip very weakly concave, adherent anteriorly. Outer lip without dentition on inner edge. Labral tooth absent. Siphonal canal open, slightly recurved to right. Siphonal fasciole strongly arched, without rostrae. Pseudo-umbilicus narrow, extending adapically beyond siphonal canal.

Holotype: UWBM 97772, DV 1628-5, lower Upper Pliocene, length (30.9) mm, width 19.6 mm.

Type Locality: Roadcut along the Panamerican Highway, 10 km south of Chala, on a winding descent from a 200 m elevation terrace towards Playa Huacllaco, locality DV 1628, north side of first sweeping outside curve from base of outcrop, south side of road, near outcrop of igneous basement rock (Figure 1), 15°52′ S, 74°10′ W (Chala 1:100,000 quadrangle).

Occurrence: Upper Pliocene, southern Peru.

Etymology: 'Paca,' Quechua for 'high,' and 'nan,' Quechua for 'path,' referring to the horizontal to concave sutural platform bordered above and below by vertical walls of the whorls.

Remarks: *Pterorytis* or *Ocinebrellus* Jousseaume, 1880, is the most appropriate genus in which to place the Huacllaco specimen, which has five varices on at least the last three whorls, consistent with the three to nine varices observed on fossil Atlantic species of *Pterorytis* (Emerson, 1959; Vermeij, 2001), the four to five varices on the modern eastern Pacific *Pterorytis hamatus* (Hinds, 1844) (Emerson, 1985), and three to twelve varices on specimens of *Ocinebrellus* (Amano and Vermeij, 1998a). The ocenebrine genera *Ceratostoma* Herrmannsen, 1846, *Pteropurpura* Jousseaume, 1880, and *Microrhytis* Emerson, 1959, in contrast, have three prominent lamellar varices on all or at least the last two whorls (Vermeij and Vokes, 1997; Amano and Vermeij, 1998a, 1998b). Specimens of *Ceratostoma*, *Pteropurpura*, *Microrhytis*, and some *Ocenebra* Gray, 1847, also have intervarical nodes, which are absent on the Huacllaco specimen and specimens of *Pterorytis* and *Ocinebrellus*.

The absence of a closed siphonal canal does not argue against assignment of the single Huacllaco specimen to *Pterorytis* or *Ocinebrellus*, since juvenile and some adult specimens of the two genera may have an open siphonal canal. The Peruvian specimen, itself partly abraded, might be a juvenile specimen or have a broken siphonal canal.

Distinguishing *Pterorytis* from *Ocinebrellus* for placement of the Huacllaco specimen is problematic. *Ocinebrellus* has four primary spiral cords on the swollen portion of the body whorl, posterior to the labral tooth, if present (Vermeij and Vokes, 1997; Amano and Vermeij, 1998a). *Pterorytis* and the Huacllaco specimen have three primary spiral cords, with an additional weak primary spiral between the shoulder and suture. On smoother specimens of both genera the number of primary spiral cords can be difficult to enumerate, and on strongly sculptured specimens the distinction between primary and secondary spiral cords is unclear if the ontogeny is unknown.

Other features are equally unsatisfactory for distinguishing the two genera. The reflection of lamellar varices is not reliable, since the lamellae may be adaperturally reflected, or not, in *Ocinebrellus* (Amano and Vermeij, 1998a), abaperturally reflected or erect in *Pterorytis* (Vermeij and Vokes, 1997), and erect or reflected in either direction on the Huacllaco specimen. The angularity of the shoulder also fails as a distinguishing character. Most specimens of *Ocinebrellus* have an angulate shoulder and a horizontal sutural platform (as is the case for the Huacllaco specimen), but some have rounded shoulders. Most specimens of *Pterorytis* have broad, planar, steeply sloping sutural platforms, but some have narrower, less inclined sutural platforms more like those of typical *Ocinebrellus* and the Huacllaco specimen.

The presence or absence of a labral tooth is not diagnostic. Some ocenebrines acquire a labral tooth only in adulthood; the Huacllaco specimen might be a juvenile. Species of *Pterorytis* that normally have a tooth (*P. umbrifer* Conrad, 1832; *P. fluviana* Dall, 1890) have specimens lacking a tooth. Specimens of *P. roxaneae* Petuch, 1994, never have a labral tooth (Vermeij and Vokes, 1997). Species of *Ocinebrellus* (sensu Amano and Vermeij, 1998a) that normally lack a labral tooth have specimens with a tooth. (In the more restrictive classification of Houart and Sirenko (2003), species of *Ocinebrellus* do not have a labral tooth.)

Taking into account this taxonomic ambiguity, the Huacllaco specimen is assigned to *Pterorytis*. Species of *Pterorytis* (*P. umbrifer*, *P. fluviana*, *P. roxaneae*) typically have smooth-shelled variants such as the specimen from Huacllaco. Most specimens of *Pterorytis*, like the Huacllaco specimen, feature a prominent primary spiral cord at the shoulder, but nonetheless usually lack spines or angulations typically seen in specimens of *Ocinebrellus*.

Pliocene Ecuadorian specimens assigned to *Ocinebrellus* by Vokes (1988) are smooth, have a prominent

shoulder spiral bordering an inclined sutural platform, and have varices that are only weakly angulate; they may be referred to *Pterorytis ecuadoria* (Olsson, 1964). They have a more fusiform profile and greater number of varices than the Huacllaco specimen.

The specimen of *Pterorytis pacanana* most closely resembles specimens of the Pliocene *Pterorytis (Pterorytis) roxaneae* Petuch, 1994, (Figures 4, 6–8) from the Pliocene Pinecrest beds of Florida (Vermeij and Vokes, 1997). Specimens of both species are thin with a waxy texture, have reduced spiral sculpture, and lack a labral tooth. Pinecrest specimens differ from the Huacllaco specimen in having four varices, not five, varical lamellae that are broader adapically, not abapically, and a weak peripheral spiral cord bordering a sloping sutural platform, rather than the strongly defined horizontal sutural platform of *P. pacanana*. Contrary to Vermeij and Vokes (1997), the holotype of *P. roxaneae* is neither excessively worn nor lacking the labral varix.

DISCUSSION

Pterorytis pacanana is the third or fourth species of *Pterorytis* recognized in the eastern Pacific Ocean, after *P. ecuadoria* (Pliocene, Ecuador), *P. hamatus* (Recent, northern Peru [Alamo and Valdivieso, 1997], a species with a protoconch unlike that of *Ocinebrellus* or any other ocenebrine [R. Houart, personal communication, 2005]), and an unnamed Recent ocenebrine from northern Peru (Radwin and D'Attilio, 1976). These taxa define an eastern tropical Pacific complement to a clade of *Pterorytis* species from the southeastern United States whose oldest members date to the late Miocene. *Ocinebrellus*, which may be endemic to the northwestern Pacific (Amano and Vermeij, 1998a; Houart and Sirenko, 2003), extends back to the Early or Middle Miocene. *Ocinebrellus* seems morphologically more similar to *Pterorytis* than other ocenebrine clades, but the trail of fossil species that might lead from Japanese *Ocinebrellus* to Panama and the Caribbean and beyond to Peruvian and Floridian *Pterorytis* has yet to be discovered (Amano and Vermeij, 1998a).

The specimen of *Pterorytis pacanana* from 16°S is remarkable for its singular occurrence and equatorial affinity. Associated taxa (Table 1) are entirely endemic or cool-water species that became prevalent after a provincial mid-Pliocene extinction that coincided with a global cooling event (Dowsett et al., 1996; DeVries, 2001). The rare appearance of *Pterorytis* in southern Peru resembles that of a mangrove bivalve, *Anadara* cf. *A. grandis* (Broderip and Sowerby, 1829), whose specimens are found in small numbers in uppermost Pliocene beds at 15°30′ S with cool-water species (Muizon and DeVries, 1985; DeVries, 1986). In a more recent example, specimens of *Chione broggi* (Pilsbry and Olsson, 1943) and *Cerithium stercusmuscarum* Valenciennes, 1833, both living today only as far south as the Sechura coastline of northern Peru (5°S) (Alamo and Valdivieso, 1997), are occasionally found in upper Pleistocene terrace deposits near San Juan de Marcona (15°20′S), Sacaco (15°30′S), and Ilo (17°40′S) (DeVries, 1986, 1988; Ortlieb et al., 1990). Ortlieb et al. (1990) proposed that the late Pleistocene thermally anomalous species were introduced southward from equatorial latitudes during El Niño events. Several such immigrations of equatorial mollusks have been documented during modern El Niños events (Arntz and Tarazona, 1990; Paredes et al., 1998). The rare Pliocene equatorial species in southern Peru were probably introduced in the same manner.

Table 1. Molluscan species associated with *Pterorytis pacanana*, new species, which was found at the base of Unit III of the Upper Pliocene beds above Playa Huacllaco, Peru. (* = Extinct).

Unit III+IV (younger)	
	Acanthina unicornis (Bruguière, 1789)
	Cancellaria buccinoides Sowerby, 1832
	Choromytilus chorus (Molina, 1782)
*	*Chorus grandis* (Philippi, 1887) / *C. giganteus* (Lesson, 1846)
*	*Concholepas camerata* DeVries, 2000
	Concholepas concholepas (Bruguière, 1789)
	Crassilabrum crassilabrum (Sowerby, 1834)
	Crepidula dilatata (Lamarck, 1822)
	Eurhomalea lenticularis (Sowerby, 1835)
	Glycymeris ovata (Broderip, 1843)
	Mesodesma donacium (Lamarck, 1818)
	Mulinia edulis (King, 1831)
	Oliva peruviana Lamarck, 1811
*	*Piscoacritia* new species
	Prisogaster niger (Wood, 1828)
	Sinum cymba (Menke, 1828)
	Xanthochorus cassidiformis (Blainville, 1832)
Unit I+II (older)	
*	*Acanthina triangularis* DeVries, 2003
*	Acmaeids
*	*Chlamys* cf. *C. vidali* (Philippi, 1887)
	Choromytilus chorus (Molina, 1782)
*	*Chorus grandis* (Philippi, 1887)
*	*Concholepas camerata* DeVries, 2000
*	*Concholepas nodosa* (Möricke, 1896)
	Fissurella spp.
*	*Herminespina mirabilis* (Möricke, 1896)
	Lithophaga sp.
*	*Piscoacritia collapsa* DeVries and Hess, 2004
*	*Stramonita* new species
*	*Tegula* (*Chlorostoma*) new species
	Xanthochorus buxeus (Broderip, 1833)
*	*Xanthochorus* new species

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A new species of *Falsimargarita* (Gastropoda: Vetigastropoda: Trochidae) from the South Atlantic Ocean

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ABSTRACT

A new trochid species, *Falsimargarita stephaniae*, is described from about 1200 m depth off the Malvinas (Falkland) Islands, South Atlantic Ocean. The new species is distinguished from the most similar congeneric ones by its exceedingly large spiral cords located only along the periphery of its shouldered whorls. A re-hydrated specimen allowed for the description of some details of the anatomy of the new species, including head-foot, buccal mass, and radula.

INTRODUCTION

Representatives of the trochid genus *Falsimargarita* Powell, 1951, can be distinguished by shell characters such as external iridescence, well-defined spiral whorls, strong spiral sculpture, opened umbilicus, and thin shell wall. The genus encompasses five species occurring in the cold or freezing deep waters off Antarctica and the Magellanic region of South America. The taxon was more recently revised by Dell (1990), who outlined the diagnostic characters of the genus and described two species.

The analysis of a specimens collected by a boat deep-fishing for king crab and tuna revealed the presence of the new species. This paper is part of a larger project of revision of western Atlantic molluscan species, which at the moment is focused on the study of deep-sea trochids.

MATERIALS AND METHODS

A single specimen with dry soft parts was available for study. Dry soft parts were carefully removed and re-hydrated in physiological solution and 3–4 drops of KOH 20% for 3 h, then transferred to 70% ETOH. Only the head-foot was adequately extracted. The dissection was performed with the specimen immersed under the fixative, in a stereomicroscope. All drawings were done under camera lucida. The radula was removed and cleaned in a boiling solution of KOH for 1 h, then cleaned by sonication in water. The examination was done under a Zeiss electron microscope at the Laboratório de Microscopia Eletrônica of Museu de Zoologia da Universidade de São Paulo.

Institutional abbreviations used in this article are: MORG, Museu Oceanográfico da Fundação Universidade de Rio Grande, Rio Grande, Brazil; MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

SYSTEMATICS

Genus *Falsimargarita* Powell, 1951

Type species: *Margarites gemma* Smith, 1915; by original designation, Antarctica.

Falsimargarita stephaniae new species
(Figures 1–12)

Diagnosis: Shell with broad spire, 5 prominent large and tall spiral cords restrict to periphery; umbilicus protected by strong plate.

Description: Shell of medium size (16.6 mm), trochoid to turbiform, whitish, iridescent-gray to pale-reddish; wall relatively thin, light. Protoconch of one smooth, glossy whorl. Separation protoconch-teleoconch poorly defined. Spire with 3.5 teleoconch whorls; each whorl highly convex, relatively high and shouldered; superior half weakly descendent, sculptured by 6–7 low and narrow spiral and numerous axial lines, both equally predominating; inferior half abruptly descendent, sculp-

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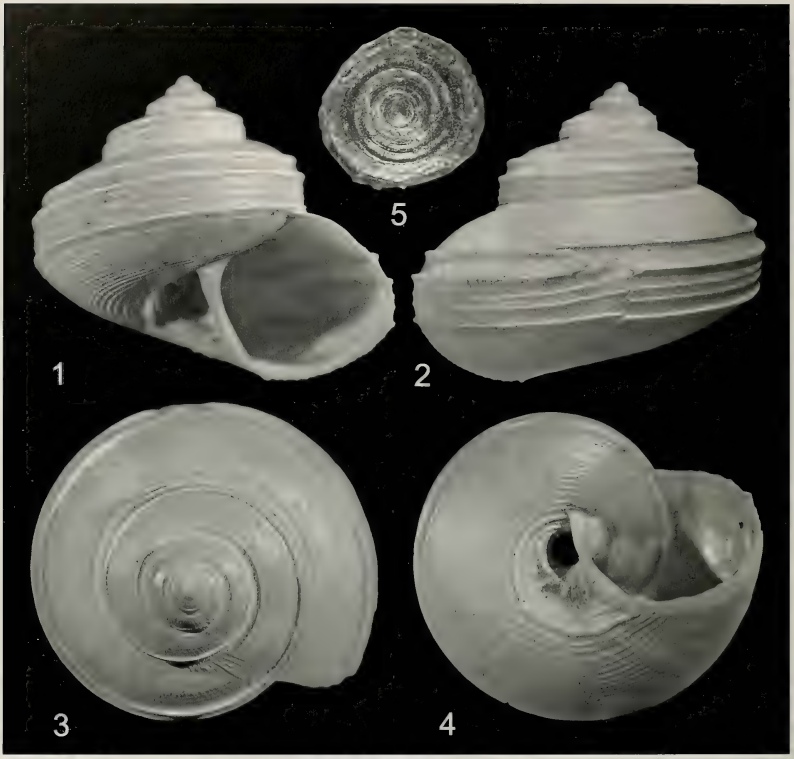
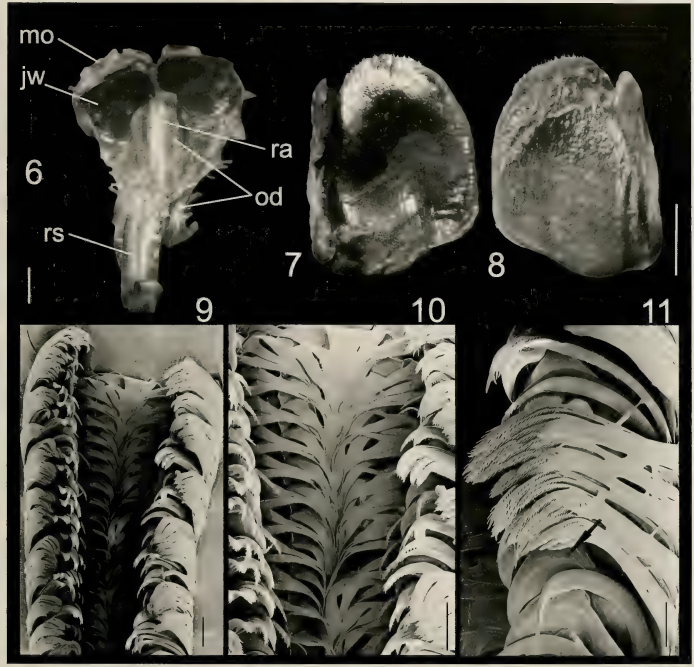


Figures 1–5. *Falsimargarita stephaniae* new species. **1–4.** Shell of holotype, apertural, abapertural, apical, and umbilical views (larger diameter 16.6 mm). **5.** Operculum, outer view.

tured by five strong and prominent spiral cords, two adapical and one abapical cords clearly larger, latter cord coinciding with suture; smooth area bearing only growth lines present between cords of abapical half of whorl. Body whorl about twice spire width, sculptured with five strong spiral cords that continue unchanged from spire; five spiral cords restricted to periphery area of body whorl; base sculptured with 18 spiral lines successively and gradually broader and more spaced toward umbilicus. Body whorl well separated from umbilicus by larger spiral cord, almost a low carina. Umbilicus open, deep, surface with simple growth lines; a strong plate-like expansion of the inner lip separates this latter from umbilicus. Aperture rounded, ample. Inner lip slightly deflected on abapical half, somewhat thick; adapical half marked only by thin glazed area on body whorl; no callus present. Outer lip rounded, thin, with small projections corresponding to spiral sculpture.

Head-foot: Total length about ½ length of last shell whorl. Head protruded, occupying about ⅓ of total head-foot volume. Snout with about ¼ of foot size,



Figures 6–11. *Falsinargarita stephaniae* new species. **6.** Buccal mass, ventral view, ventral wall opened longitudinally along median line and deflected to expose jaws. Scale bar = 1 mm. **7–8.** Left jaw plate, outer and inner views. Scale bar = 0.5 mm. **9–11.** Radula. **9.** General view; **10.** Detail of central and lateral teeth. Scale bars = 100 µm. **11.** Detail of lateral teeth, arrow indicating fifth lateral tooth. Scale bar = 50 µm. Abbreviations: **jw,** jaw; **mo,** mouth; **od,** odontophore; **ra,** radula; **rs,** radular sac.

cylindrical, broad; distal surface flattened, fully covered with small papillae; each papilla cylindrical, tip rounded; mouth central. Tentacles long (about twice snout length), narrow, tip rounded. Ommatophore with about ¼ of tentacle length and approximately with same width; located just posterior to tentacles; eyes dark, on ommatophore tips. Foot occupying about ⅔ of head-foot volume. Mesopodium constituting most of foot, outline somewhat triangular; sole flat, simple; anterior furrow of pedal glands bordered by thick margins, restricted anteriorly, not protruding beyond lateral edges. Epipodium divided into two apparently symmetrical lateral flaps, covering entire dorsal surface of mesopodium, from snout base to opercular pad; bearing eight pairs of long epipodial tentacles projecting about twice longer than epipodial width, each tentacle protruding on ventral but not on dorsal epipodial surface; each epipodial tentacle bearing papillae at ventral surface of basal region; papillae increasing in number and size toward middle tentacles; some epipodial tentacular papillae bifid at tip. Opercular pad with edges as continuation of epipodium. Columellar muscle thick, encompassing a half whorl.

Operculum: Circular, horny, multispiral; nucleus central; occupying entire shell aperture.

Digestive System: Buccal mass somewhat larger than snout internal space. Buccal cavity having a pair of very large, dark-brown jaw plates, outline somewhat elliptical,

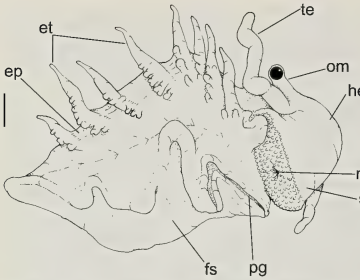


Figure 12. *Falsimargarita stephaniae* new species. Head-foot, ventral to slightly lateral right view, epipodium deflected upward. Scale bar = 1 mm. Abbreviations: **ep,** epipodium; **et,** epipodial tentacle; **fs,** foot (mesopodium) sole; **he,** head; **mo,** mouth; **om,** ommatophore; **pg,** anterior furrow of pedal glands; **sn,** snout; **te,** cephalic tentacle.

both jaws occupying most of dorsal and lateral surfaces of buccal cavity; posterior and lateral regions of jaws low, medial and anterior regions taller, with projected edges; series of small cusps present along anterior and medial edges, each cusp pointed and well separated from each other. Odontophore about half projected into buccal cavity. Radular ribbon about three times odontophore length; about half of radular ribbon projected beyond posterior end of odontophore.

Radula: Rachidian tooth encompassing about ¼ of radular ribbon width, triangular, narrowing somewhat abruptly, strongly curved over its own base; cutting edge sharply pointed, margins with very slender, elongated cusps. First to fourth lateral teeth long, slender, narrowing gradually, curved inward; distal half bearing edges with slender, elongated cusps; tip sharply pointed. Rachidian and four more central lateral teeth thin, flexible. Fiftieth lateral tooth thick, hook-like, curved inward; base broad, thick; distal region arched, resembling a thick scythe. Marginal teeth slender, tall, about 20 pairs per row, slightly broader toward medial region; base ruler-like, weakly curved inward; distal half sharpening gradually, with several slender, elongated cusps along edges about 25 pairs per tooth; tip sharply pointed.

Holotype: MORG 49650 (shell and operculum), MZSP 46559, diameter: 16.6 mm; height: 14.6 mm; includes re-hydrated soft parts and radula.

Type Locality: Argentina, off Islas Malvinas (45°S 58°W), 1200 m depth (fishing boat col., x/2004, Helen Racz leg.).

Distribution: Known only from type locality.

Etymology: The Latinized specific epithet honors the collector's mother, Ms. Teodora Stefania.

DISCUSSION

Although it has been recognized that definitions of generic boundaries in the Trochidae merits further revision, we are reasonably certain of its generic allocation of the new species, because the species possesses the conchological attributes reported in the Introduction for *Falsimargarita*.

There are two other genera also occurring in the South Atlantic Ocean that also exhibit iridescent shells, a character associated with the presence of thin outer shell layers. One of these genera is *Margarella* Thiele, 1893 (see Zelaya, 2004); the new species cannot be allocated into this genus because of its larger size, presence of thin shell wall, and absence of a parietal callus. The other genus is *Gaza* Watson, 1879; *Falsimargarita stephaniae* can not be included in *Gaza* given its taller shell, more rounded spiral whorls, and absence of a flap covering the umbilicus.

Additional comparisons and discussion about *Falsimargarita* is provided by Dell (1990: 93). At first glance, the new species could also be assigned to the Indo-Pacific genus *Otukaia* Ikebe, 1942; however, the new species has lower profile, more elaborate sculpture, and a more widely open umbilicus.

Falsimargarita stephaniae differs from the remaining congeneric species *F. iris* (Smith, 1915), *F. gemma* (Smith, 1915), *F. thielei* (Hedley, 1916), *F. georgiana* Dell, 1990 and *F. benticola* Dell, 1990) by having shouldered whorls, and by the strength of the spiral folds. The other species have a rounded whorl profile and a uniformity of spiral sculpture. Only *F. thielei* possesses differentiable spiral cords resembling those of *F. stephaniae*; however, *F. stephaniae* additionally differs from *F. thielei* by having a larger number of those outstandingly large spiral cords at the shell periphery and a taller spire.

The bathymetry is also a distinctive among *Falsimargarita* species. *Falsimargarita gemma, F. iris*, and *F. thielei* occur in depths to 400 m. *Falsimargarita benthicola* and *F. georgiana* are found in deeper waters around 3000 m, while *F. stephaniae* occurs at intermediary depths, around 1200 m.

Until the discovery of the new species, the only *Falsimargarita* known to occur in latitudes north of 50°S was *F. iris*, which reaches 35°S (Rosenberg, 2004). *Falsimargarita stephaniae* is the second species recorded for these latitudes.

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BIVALVIA 2006 - INTERNATIONAL CONGRESS ON BIVALVIA, BELLATERRA (BARCELONA), SPAIN, 22–27 JULY 2006

The congress, to be held at the Universitat Autònoma de Barcelona, calls together neontologists and palaeontologists with research interests in bivalve mollusks. Plenary talks include population genetics, evolution of ontogeny, evolutionary paleontology, biomineralization, and freshwater conservation biology, but contributions need not be restricted to these topics. In addition, there will be a planning session for a new bivalve treatise.

Two one-day excursions—one each on recent and fossil bivalves—will be organized.

Interested parties are asked to register and submit abstracts via the congress webpage http://bivalvia2006.uab.es.

Further inquiries may be directed to Niko Malchus (n.malchus@gmx.net). Please include in the subject line "Bivalvia 2006".

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2006 MEETINGS OF THE AMERICAN MALACOLOGICAL SOCIETY AND THE WESTERN SOCIETY OF MALACOLOGISTS, SEATTLE, WASHINGTON, 29 JULY–3 AUGUST 2006

The 72nd annual meeting of the American Malacological Society and the 39th annual meeting of the Western Society of Malacologists will be held jointly in Seattle from 29 July–3 August 2006 under the coordination of AMS and WSM co-president Dr. Roland C. Anderson. The meeting's main venue will be the University of Washington. Reasonably priced housing will be available at the University dormitories and the University Inn Motel. The opening night reception will be held at the Burke Museum, located on campus, and the closing banquet will be at UW's University Club, also on campus. Thursday, 3 August, will be devoted to field trips.

The meeting will include three symposia: one on cephalopod behavior organized by Jennifer Mather of the University of Lethbridge, one on chitons organized by Douglas Eernisse of the California State University at Fullerton, and one on opisthobranchs organized by Sandra Millen of the University of British Columbia, Canada.

There will be a sale of malacological reprints to benefit the student fund of WSM and the traditional spirited auction of books and molluscan memorabilia (no shells) that will benefit the student funds of both organizations. Several notable items of cephalopod art have already been donated as well as a copy of R. T. Abbott's 2nd edition of American Seashells. Bring some of your reprints, books, and molluscan art to benefit this very worthy cause! Reprints and auction items can be sent to Roland Anderson at the address below.

For further information please contact AMS and WSM president:

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Seattle, WA 98101 USA
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THE NAUTILUS

Volume 119
2005

AUTHOR INDEX

Ardila, N. E. 157
Barwick, K. 43
Carbonini, A. K. 157
Carpenter, S. 105
Carranza, A. 83
DeVries, T. J. 164
Glaubrecht, M. 15
Díaz, J. M. 157
Harasewych, M. G. 149
Hartfield, P. D. 1
Ituarte, C. 93
Kantor, Y. I. 149
Köhler, F. 15, 90
Mariottini, P. 109
Miloslavich, P. 157
Minton, R. 11
Nielsen, S. N. 153
Norbis, W. 83
Rios, E. C. 169
Pastorino, G. 55
Roe, K. J. 1
Rolán, E. 109
Roth, B. 116
Saul, L. R. 133
Savarese, S. P. 11
Simone, L. R. L. 169
Slapcinsky, J. 27
Smriglio, C. 109
Squires, R. L. 133
Strong, E. E. 119
Valdés, Á. 43, 91
Vilvens, C. 50

NEW TAXA PROPOSED IN VOLUME 119 (2005)

GASTROPODA

Akera julieae Valdés and Barwick, 2005, new species (Akeridae) 44
Bullamirifica Squires and Saul, 2005, new genus (Indeterminate family) 137
Bullamirifica elegans Squires and Saul, 2005, new species (Indeterminate family) 140
Bullamirifica verruca Squires and Saul, 2005, new species (Indeterminate family) 138
Calliotropis pulvinaris Vilvens, 2005, new species (Trochidae) 50
Coralliophila trigoi Mariottini, Smriglio and Rolán, 2005, new species (Muricidae) 110
Daffymitra Harasewych, 2005, new genus (Volutomitridae) 149
Daffymitra lindae Harasewych, 2005, new species (Volutomitridae) 150
Exilia alanbeui Nielsen, 2005, new species (Ptychatractidae) 154
Falsimargarita stephaniae Rios and Simone, 2005, new species (Trochidae) 169
Minutropis Squires and Saul, 2005, new genus (Capulidae) 143
Minutropis melilota Squires and Saul, 2005, new species (Capulidae) 143
Nerita orovillensis Squires and Saul, 2005, new species (Neritidae) 136
Paryphantopsis abstrusa Slapcinsky, 2005, new species (Charopidae) 29
Paryphantopsis koragae Slapcinsky, 2005, new species (Charopidae) 31
Paryphantopsis lebasii Slapcinsky, 2005, new species (Charopidae) 33
Paryphantopsis matawanensis Slapcinsky, 2005, (Charopidae) 35
Paryphantopsis ubwamensis Slapcinsky, 2005, new species (Charopidae) 37
Paryphantopsis yawii Slapcinsky, 2005, new species (Charopidae) 39
Paxitropis Squires and Saul, 2005, new genus (Capulidae) 144
Paxitropis dicriota Squires and Saul, 2005, new species (Capulidae) 144
Pterorytis pacanana DeVries, 2005, new species (Muricidae) 165
Tegula jeanae Squires and Saul, 2005, new species (Trochidae) 135
Trophon parodizi Pastorino, 2005, new species (Muricidae) 76

BIVALVIA

Hamiota Roe and Hartfield, 2005, new genus (Unionidae) 1
Pisidium chicha Ituarte, 2005, new species (Sphaeriidae) 100
Pisidium ocloya Ituarte, 2005, new species (Sphaeriidae) 97
Pisidium omaguaca Ituarte, 2005, new species (Sphaeriidae) 94

REVIEWERS FOR VOLUME 119

Philippe Bouchet
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